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Understanding the key ecological traits of cyanobacteria as a basis for their management and control in changing lakes

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Abstract Anticipated climatic changes combined with eutrophication are predicted to enhance the dominance of several notorious cyanobacterial taxa. Cyanobacteria have many key ecological traits that may allow them to thrive under foreseen scenarios of environmental change. Understanding the ecophysiological traits of harmful species has proven important for their successful control and management. Indeed, if the links between key cyanobacterial traits and the specific environmental conditions that allow expression of these traits can be disrupted, we could identify (novel) means for operational control and mitigate or prevent water quality problems. A good example is artificial mixing of a lake that breaks down the water column stability on which fast floating, buoyant cyanobacteria depend. Based upon Reynolds' functional phytoplankton classification, we focused on five groups of cyanobacteria that from a management point of view can be seen as homogeneous and have comparable environmental sensitivities. For each group, we present (1) its key traits, (2) how these characteristics will maintain their function under future environmental change, (3) explanation of how understanding the function of these traits can reveal the "Achilles heel" of the particular functional group and (4) which (combination of) control measures is most likely to be successful. Despite looking for specific environmental sensitivities of individual groups, we maintain that controlling nutrients remains the basis for managing blooms, no matter which functional type dominates. Providing further ecological knowledge to lake management could be the key to effective bloom control and healthier, sustainable freshwater ecosystems even in a warmer future.

Keywords Climate change · Cyanobacterial blooms · Eutrophication · Functional traits · Lake management · Microcystins

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Introduction

This publication is the first paper in a special issue of Aquatic Ecology on "Cyanobacterial blooms: Ecology, prevention, mitigation and control." In this special issue, the various contributions discuss a range of control measures available to lake management to prevent and control nuisance blooms of cyanobacteria.

In this contribution, we review what is known about those key traits of cyanobacteria, like buoyancy or nitrogen fixation that define their ecological niche and are key to their successful management. Our title, however, also speaks of "changing lakes," and we cannot properly address cyanobacterial problems without discussing the—changing—environment they live in. So this publication also outlines the main consequences of eutrophication and climate change, as two major drivers of bloom formation.

Phosphorus and nitrogen pollution is the biggest threat to water quality worldwide (Schindler and Vallentyne 2008). Anthropogenic eutrophication from sewage, fertilizers and detergents is responsible for massive algal blooms that capitalize on the excess of nutrients. Cyanobacterial blooms are the most conspicuous sign of eutrophication, mostly resulting in a strong smell, discoloration of the water and accumulation of floating cyanobacteria at the lake surface (Ibelings and Chorus 2007). Highly eutrophic waters can support excessive cyanobacterial biomass that increases turbidity, limits the penetration of light to deeper layers and increases anoxia in the hypolimnion (Schindler et al. 2008). Managers have worked hard to control eutrophication. The International Lake Environment Committee's (ILEC) review on 217 lakes showed that water management in industrialized areas succeeded in reducing nutrient input in many lakes (e.g., Lake Biwa—Japan, Lake Constance—Germany and Switzerland, Lake Balaton—Hungary, the Great Lakes in North America), but the nutrient concentrations did not yet return to the levels of the 1950s, before the peak in the eutrophication, and in many lakes with high historical loads, internal loading will continue to fuel cyanobacterial blooms for many years after external nutrient inputs have been reduced. In many cases, for instance, Lake Veluwe—the Netherlands—lakes showed severe hysteresis to restoration measures and remained in a turbid state for decades, despite tackling external nutrient loading (Ibelings et al. 2007).

An important question is which nutrient, phosphorus or nitrogen, is chiefly responsible to promote cyanobacterial biomass in an ecosystem. Schindler et al. (2008) proved experimentally that algal blooms in the eutrophic lakes they studied could not be controlled by reducing nitrogen input, but only by managing phosphorus. According to their whole-ecosystem experiment, reducing nitrogen inputs

increasingly favored nitrogen-fixing cyanobacteria that outcompeted the other phytoplankton. Nitrogen fixation could sustain cyanobacterial biomass and the lake remained highly eutrophic, despite showing indications of extreme nitrogen limitation seasonally (Schindler et al. 2008). But this shift to nitrogen fixers does not occur in most N-limited lakes of low to moderate fertility, and where it does, lakes typically remain N limited despite the presence of nitrogen fixers (Paerl et al. 2011). N_2 fixation can only sustain <50 % of primary production, even when P supplies are sufficient (Scott and McCarthy 2010). Furthermore, there are records of eutrophic systems dominated by non-N_2 fixers that are N and P co-limited or even N limited (Paerl et al. 2011). Rigosi et al. (2014) showed that both nutrients are dominant factors promoting blooms. Thus, the feasibility of focusing only on P deficiency must be evaluated on a case-by-case basis (Lewis and Wurtsbaugh 2008) since it is likely that both N and P input controls are needed for long-term cyanobacterial bloom management. Indeed, we emphasize that nutrient control always needs to be the basis of lake restoration measures, aimed to reduce or prevent problems caused by algal blooms.

There is mounting evidence that the current worldwide increase in cyanobacterial blooms is not just the result of anthropogenic eutrophication. Climate change, through direct and indirect effects of warming, is seen to play an increasing role in changing the properties of the aquatic ecosystems (Elliott 2012; Kosten et al. 2012; Paerl and Huisman 2008). Global warming has the potential to directly affect phytoplankton community composition as the growth rates of different phytoplankton taxa exhibit different optimal ranges (Butterwick et al. 2005). Apart from the direct consequences of warming, the increase in surface water temperature in peri-alpine lakes, for instance, has resulted in up to 20 % higher water column stability (Livingstone 2003). As a consequence of global warming, the thermocline of deep stratifying lakes remains stable for longer periods (earlier onset in spring, later and incomplete overturn in autumn) and becomes positioned at shallower depths, potentially enhancing the growth of certain cyanobacterial taxa (Paerl and Huisman 2008). Intensified vertical density stratification reduces vertical mixing resulting in enhanced scope for buoyancy-controlled vertical positioning of cyanobacteria (Paerl et al. 2011). Under stable water column conditions,

positively buoyant cyanobacteria will be able to regulate their position in the water column and remain in the euphotic zone, while non-motile, negatively buoyant algae that can only remain suspended in the water column under mixing conditions will tend to sink (Reynolds 1984; Bormans and Condie 1998). Moreover, being closer to the lake surface, buoyant cyanobacteria are closer to the source of CO_2, diffusing in from the atmosphere (Paerl et al. 2011). Higher atmospheric carbon dioxide concentrations will result in higher dissolved carbon dioxide concentrations that may (partly) relieve the potential C limitation of the cyanobacteria with higher cyanobacterial biomass as a consequence (Verspagen et al. 2014). Microelectrode studies, however, demonstrated that the local demand for carbon in cyanobacterial surface waterblooms far outstrips the supply, resulting in severe C limitation, despite being at the surface (Ibelings and Maberly 1998).

Furthermore, climate change may affect the occurrence of cyanobacterial blooms in other, perhaps more subtle ways. We give a few examples. Changes in precipitation are expected due to global warming (IPCC 2007). Intensified precipitation will result in higher terrestrial runoff, increasing nutrient input and stimulating blooms. Increased flushing rates, on the other hand, may prevent blooms when lake residence times are reduced to very low values (Verspagen et al. 2006), but ultimately enhanced nutrient loads always carry a risk of promoting blooms (Paerl and Huisman 2008). Droughts may reduce the flow rate of major rivers to values low enough to support cyanobacteria as found in many Australian rivers (Bormans et al. 2005; Viney et al. 2007), and this may increase their presence in the potamoplankton, even in temperate regions, as demonstrated for the rivers Rhine and Meuse in extremely warm and dry summers (Ibelings et al. 1998). According to the World Meteorological Organization's 2013 report, the occurrence of some extreme events (e.g., hurricane Katrina in 2005 or floods in Pakistan in 2010) can be attributed to climate change (www.cgd.ucar.edu/cas/ace/). The impact of extreme events, like summer heat waves as occurred in Europe in 2003 on lake ecosystems, is likely to be different from the effects of long-term gradual warming (Anneville et al. 2010; Gallina et al. 2011; Straile et al. 2010), but not all summer heat waves, for instance, were shown to promote blooms of cyanobacteria (cf. Jöhnk et al. 2008 vs. Anneville et al. 2015).

We have thus identified eutrophication and climate change as two major anthropogenic stressors that may favor cyanobacterial blooms. These two factors have a clear impact on algal blooms by themselves, but they do not necessarily work only independently. A high algal biomass in eutrophic systems, for instance, can increase the water temperature at a local scale due to strong light absorption (Ibelings et al. 2003). Consequently, eutrophication may promote warmer water and provide additional competitive advantage of buoyant over non-buoyant phytoplankton (Paerl and Huisman 2008; Fig. 1). The underwater light climate as experienced by the phytoplankton is determined by two factors: light attenuation and mixing depth. Steep light attenuation in eutrophic lakes limits the availability of light to a shallow euphotic zone. Climate warming decreases the mixing depth, shifting the advantage to buoyant cells that can float up into the illuminated near-surface mixed layer (Ibelings et al. 1991; Fig. 1). These surface blooms will further increase the underwater light extinction coefficient (Fig. 1). These examples demonstrate the potential for eutrophication to ally with climate warming in promoting the conditions for cyanobacterial growth and dominance (Moss et al. 2011).

The general expectation is that ongoing climate change will amplify eutrophication problems, but much uncertainty remains about the extent to which both stressors will interact. These two stressors may interact in different modes, additive, antagonistic or synergistic. Specifically, it remains an open question whether nutrient and temperature will interact synergistically, so that the combined effects of eutrophication and global warming will be worse than the effect of each single factor alone. Several authors, either through the use of long-term monitoring data or in modeling simulations, have studied the interaction between eutrophication and climate warming as important drivers of blooms (Elliott et al. 2005; Wagner and Adrian 2009). Studies by Kosten et al. (2012), Posch et al. (2012) and Paerl and Huisman (2008) point to higher temperatures combined with nutrients inputs as being important for cyanobacterial bloom formation. However, Jeppesen et al. (2005), using long-term data from 35 lakes located from the subtropical to the temperate zone in North America and Europe, argued that phytoplankton composition is primarily driven by nutrient loading, with global warming effects less detectable. Recent work by
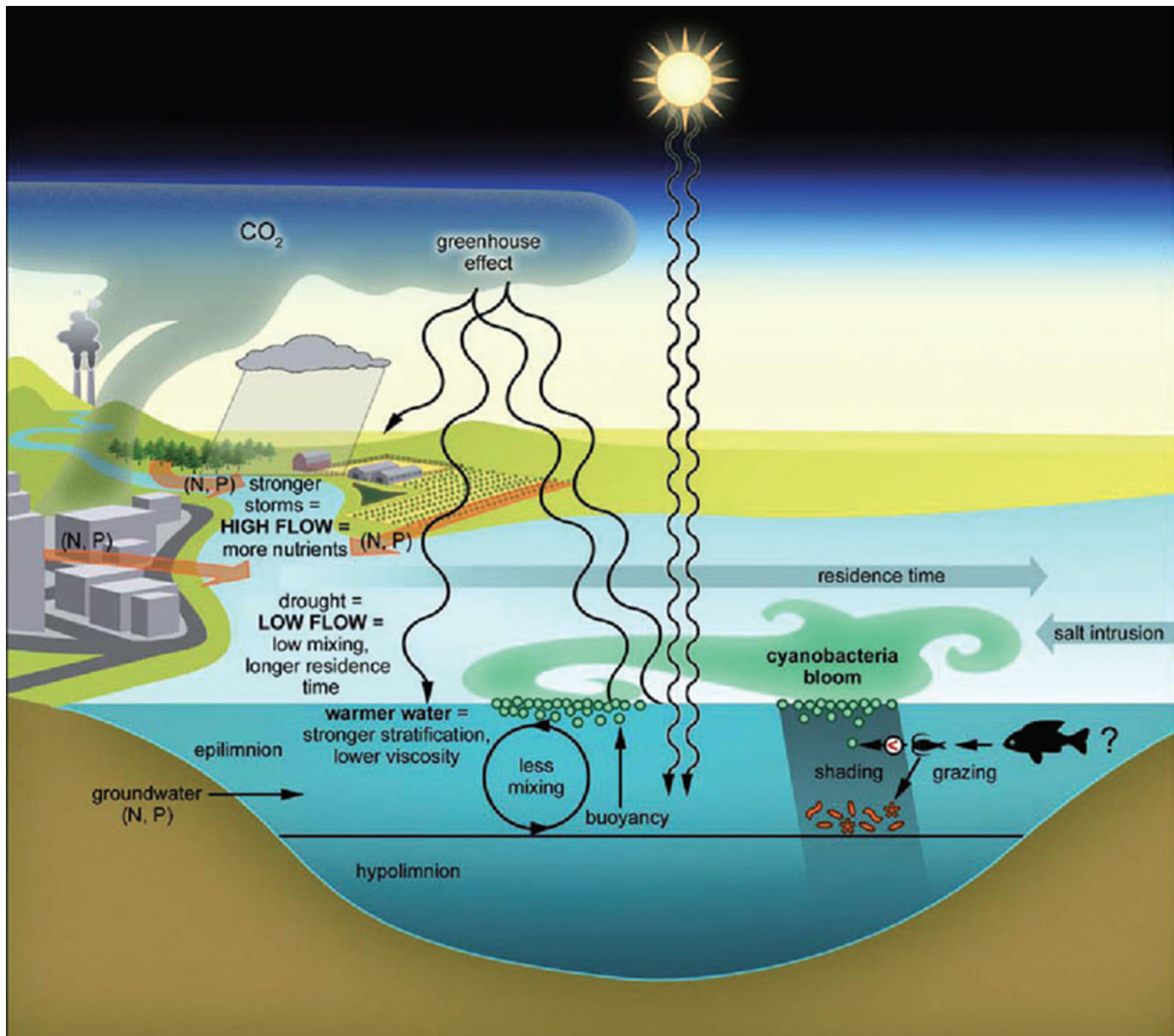
Fig. 1 Conceptual figure, illustrating the environmental controls of cyanobacterial bloom dynamics, and the direct and indirect effects of climate change on these dynamics in combination with external nutrient loading. Figure taken from Paerl and Huisman (2009) with permission by Wiley Journals

Rigosi et al. (2014) on ca. 1000 American lakes showed that both nutrients and temperature are main determinants of variation in cyanobacterial occurrence between lakes, but they found no overall support for a significant synergistic interaction between nutrients and temperature on cyanobacterial biomass. Moreover, the relative importance of these two factors and their interaction was clearly dependent on lake trophic state and dominant cyanobacterial taxa. Apparently, there is no scientific consensus on the importance and mode of interaction between nutrients and temperature and further investigations are needed. Cyanobacterial blooms are very persistent, and we need to work on better solutions to limit their occurrence and to control their impacts on lake ecosystems and the crucial ecosystem services they provide (Cardinale et al. 2011).

Cyanobacteria and their key traits

Ecology, as a predominantly biological discipline, is concerned with the distributions of organisms and their interrelationships as well as the interactions with their environment (Reynolds et al. 2002). Phytoplankton possesses a high diversity of well-defined

ecological traits that can vary predictably over different environmental gradients. Trait-based approaches in ecology demonstrate the importance of functional diversity in determining key properties of ecosystems and their functioning (Litchman and Klausmeier 2008). Typically, planktonic food webs are characterized by a high degree of redundancy indicating a strong functional similarity among species, with a small proportion of species exerting disproportionally strong effects on lake ecosystem functioning (Woodward 2009). Therefore, an important but not yet fully resolved question in the study of biodiversity and functioning of freshwater ecosystems is not what species are (species identity), but what species do (functional role) (Hillebrand and Matthiessen 2009; Suding et al. 2008). This implies that assemblages of organisms should be characterized based on phenotypic functional traits that respond directly to environmental changes (response traits) and determine the effects on aggregated processes at the community and ecosystem level (effect traits). Several studies have shown how key traits can favor the occurrence of trait holders under defined sets of environmental conditions. This includes blooms of nuisance cyanobacteria, where decades of study have resulted in a fair understanding of how key traits determine the occurrence of the main bloom forming taxa (Dokulil and Teubner 2000). Therefore, lake management needs to explore ways to disrupt the conditions where cyanobacteria benefit from these traits, in order to better control bloom dynamics. Understanding the ecology of harmful species and their key traits proved already successful for their control and management in cases like the hypertrophic Lake Nieuwe Meer in the Netherlands (Visser et al. 1996), where artificial mixing removed the water column stability on which buoyant *Microcystis* depended. Ecology can provide the right guidelines for controlling nuisance harmful blooms and inform new technological measures.

Cyanobacteria, formerly known as blue-green algae, are the Earth's oldest known oxygenic photoautotrophs, and they have a global distribution (Cheung et al. 2013). Cyanobacteria are prokaryotic organisms that may occur as large colonies or filaments in lakes giving them a greater resistance to grazing (Reynolds 2006). They contain chlorophyll a like all other phytoplankton taxa and specific accessory pigments, such as phycocyanin or phycoerythrin (Glazer 1984), that can help them to adapt to the available light conditions (Tandeau de Marsac 1991). Cyanobacteria have several more ecophysiological adaptations that allow them to dominate aquatic systems under changing environmental conditions (Carey et al. 2012). For example, some cyanobacteria produce gas vesicles (Walsby 1994) that allow them to regulate their buoyancy (Ganf and Oliver 1982; Hudnell and Dortch 2008; Huisman et al. 2006). Under the increased thermally stratified conditions, which are anticipated with global warming, these cyanobacterial taxa might be able to migrate between well-illuminated surface layers and nutrient-rich hypolimnetic waters (Ganf and Oliver 1982), escaping the increasingly nutrient-depleted epilimnia of lakes during extended stratification periods (Livingstone 2003). See, however, Bormans et al. (1999) reporting that no studies provide support for migration to sufficient depths to access nutrients in stratified systems. Cyanobacteria may also take direct advantage of warming because their growth rate will continue to increase with temperature, while the growth rates of many other phytoplankton taxa decline over 20 °C (Litchman et al. 2010; Reynolds 2006). See Lürling et al. (2013), however, who found no significant differences in optimum growth temperatures between cyanobacteria and green algae. Other key traits such as the ability to fix nitrogen (Oliver and Ganf 2000; Reynolds 2006) and to produce dormant cells as a means to survive unfavorable conditions (Bartram and Chorus 2002) can provide cyanobacteria with a competitive advantage over other phytoplankton (Carey et al. 2012; Litchman et al. 2010), especially under increasingly unpredictable future climate conditions (IPCC 2007). See further discussion of these traits when we list the various cyanobacterial functional groups.

Cyanobacteria are responsible for numerous problems with high environmental and socioeconomical impacts. Cyanobacterial blooms, like all high algal crops, have considerable negative effects on aquatic food webs and ecosystem functioning by turning lakes anoxic, inducing fish mortality, reducing diversity and increasing habitat loss (Chorus and Bartram 1999; Havens 2008; Paerl et al. 2011). There is a growing concern that the frequency and magnitude of cyanobacterial blooms will be enhanced globally (Huber et al. 2012; Jöhnk et al. 2008) and that the geographic range of some cyanobacterial species will expand (Briand et al. 2004; Ryan et al. 2004; Sinha

et al. 2012). Many cyanobacterial taxa produce various types of toxins, such as hepatotoxins, neurotoxins and dermatotoxins (Carmichael 1997). These toxins present a considerable risk to drinking water (Codd et al. 2005) and pose a substantial economic cost (Dodds et al. 2009; Steffensen 2008). The World Health Organization (WHO 1996) has been gathering information on toxic cyanobacteria including issues of human health, safe water practices, management, prevention and remediation. Toxic water blooms in many eutrophic to hypereutrophic freshwater ecosystems (sometimes also in low nutrient levels) worldwide are responsible for sporadic but recurrent episodes of wild and domestic animal illness and death as well as for occasional human poisonings from municipal and recreational water supplies (Carmichael 2001). Toxic and non-toxic strains can coexist within a population (Kurmayer et al. 2002; Kardinaal et al. 2007; Briand et al. 2008). Experiments with *Microcystis* showed that increased temperatures independently and in interaction with elevated phosphorus concentrations can yield more toxic strains of *Microcystis* than non-toxic ones suggesting that nutrient loading and global warming may additively promote blooms with higher microcystin content (Davis et al. 2009). However, previous experiments with *Planktothrix agardhii* have shown that increased temperatures do not result in an increase in toxin production, while high nitrogen concentrations affected the increase in both toxic and non-toxic strains (Sivonen 1990). In these experiments though, the interaction between temperature and nutrients was not tested.

Although cyanobacteria share certain key traits, they are a heterogeneous group, in which each taxon possesses different ecophysiological adaptations. For example, the size range of a cyanobacterial unit spans nearly five orders of magnitude (from the smallest single-celled cyanobacterial picoplankton to the multi-cellular filaments and colonies); the photosynthetic rates and growth rates of different taxa vary widely (Reynolds et al. 2002). Different combinations of these morphological and physiological traits might result in varied responses to changes in temperature and nutrients. Plasticity of these traits arises from differential gene expression within species and results in higher diversity of trait values (Litchman et al. 2010). Plastic responses reflected in morphological traits occur on a range of timescales from sub-second (e.g., re-arrangements in the light-harvesting antenna)

to days (e.g., augmentation of the gas vesicle volume) in response to the prevailing environmental situation (Ibelings et al. 1994; de Tezanos Pinto and Litchman 2010a). While phenotypic plasticity can be advantageous under changing environmental conditions, it is dependent on a match between timescales of environmental fluctuations and plastic responses (Stomp et al. 2008). Thus, if an environmental disturbance occurs too fast, the cyanobacterial species present at the moment might not be as quick as necessary to adapt to the new conditions. This functional plasticity and its variation between cyanobacterial taxa have to be taken into account if we want to properly understand their behavior and achieve an effective control of toxic cyanobacterial blooms.

Functional classification of cyanobacteria

Trait-based approaches are gaining in popularity, given their opportunity to explain and predict group distributions along environmental gradients. It has been argued that patterns of functional diversity may afford better insights into processes of ecosystem change and responses (Reiss et al. 2009). Recognizing how key traits can enable the proliferation of certain species or functional groups can help to predict which cyanobacterial taxa are most probably going to increase disproportionally under eutrophication and global warming (Litchman et al. 2010). Trait-based phytoplankton ecology arguably started with Margalef (1978) (however also read Lund, 1965) who predicted the occurrence of different taxonomic/functional groups of phytoplankton along gradients of nutrients and turbulence. A more detailed trait-based approach was developed by Reynolds (2002, 2006) who catalogued the natural assemblages of phytoplankton species, of contrasted water bodies with specific trophic status, according to their morphological and physiological key traits. Litchman and Klausmeier (2008) proposed the use of ecologically relevant traits of phytoplankton (morphology/cell size, temperature and reproduction-related traits) as fundamental data to be integrated in mathematical models for predicting community structure under changing environmental conditions. Kruk et al. (2011) tested a morphology-based functional groups classification against environmental conditions, for a large dataset (211 lakes) covering a wide range of conditions, while Fraisse et al. (2013) explained

differences in phytoplankton community structure in rivers using a morphofunctional approach. Carey et al. (2012) gathered information about specific ecophysiological key cyanobacterial traits (ability to grow in higher temperatures; buoyancy; high affinity for and ability to store phosphorus; nitrogen fixation; akinete production; efficient light harvesting) that are predicted to enhance cyanobacterial dominance under future climate scenarios. In this paper, we will use Reynolds (2006) functional classification, which is an update to the Reynolds et al. (2002) publication, specifically for the cyanobacterial taxa in there. We will focus on five selected functional groups that include taxa of concern such as *P. agardhii*, *Cylindrospermopsis raciborskii*, *Anabaena flos-aquae* (now *Dolichospermum flos-aquae*; Wacklin et al. 2009), *Microcystis aeruginosa* and *Planktothrix rubescens*, and show how trait-based cyanobacterial ecology can be used for our benefit in the management of these harmful blooms.

Reynolds (2006) treated his phytoplankton species-counts as phytosociological relevés (small areas of uniform vegetation according to Tüxen 1955) and diagnosed the species that were co-occurring frequently, rarely or not at all. The different clusters were categorized in an alphanumeric system that conveniently suits the patterns and periodic sequences of the natural assemblages in a given lake. Reynolds' Table (2006) (presented in a shortened and revised version in Table 1) enlisted the typical representatives of each particular phytoplankton association, which demonstrate similar morphologies and the habitat type where they are typically encountered. Additionally, the environmental tolerances and the related key functional traits of each group are enlisted, providing an idea on what to expect in response to environmental change. For the purpose of this paper, the table identifies the environmental sensitivities of each group, which can in theory be exploited to compose dedicated management solutions (referred to by us as the "Achilles heel" of each group). In Table 1, we enlist only eight out of the 31 groups of Reynolds' phytoplankton associations (those containing the major bloom forming taxa), from which several were combined to form three groups (S_1/S_2; H_1/H_2; L_O/L_M); additionally, we retain S_N and R as separate groups. We combined the aforementioned associations into three groups, based upon the conviction that from a management/control point of view these can be treated as homogeneous groups, with comparable environmental sensitivities. Further down we discuss the five groups in Table 1 by choosing one main representative per group, akin a holotype in taxonomy, that is of specific interest from an ecological and management point of view. For each group, we first discuss its key traits, then how the use of these key traits may be altered by environmental (climate) change, then whether and how understanding the key traits opens up opportunities for the management and control of the functional group in question and finally which—combination—of control measures may actually be most likely to successful.

S_1/S_2: Turbid mixed layers—*Planktothrix agardhii*

Key traits

The representative species in S_1/S_2 (Table 1) are efficient light harvesters that have the ability to grow successfully under light-limited conditions by adjusting their pigment composition effectively in response to the ambient irradiance (Fietz and Nicklish 2002). In this paper, we focus on *P. agardhii* that dominates very turbid lakes. The populations of *P. agardhii* can be maintained throughout the year when the winter temperatures are mild (Sas and Ahlgren 1989). Filamentous cyanobacterial species such as *P. agardhii* are superior in light harvesting compared to larger colonial species, mostly due to morphological adaptations such as their slender, attenuated form (Reynolds 2006). *P. agardhii* requires little energy to maintain cell function and structure; thus, it is capable of maintaining its biomass under light-limiting conditions (Van Liere and Mur 1979). *P. agardhii* may produce microcystins (e.g., Tonk et al. 2005).

Key traits under eutrophication and climate change

Climate warming can favor the dominance of *P. agardhii* since experiments have shown that its growth can increase steeply in a temperature range from 10 to 30 °C (Foy et al. 1976). Eutrophication, on the other hand, stimulates dense blooms that reduce light availability in the water column and support *P. agardhii* populations (Carey et al. 2012). In highly enriched shallow waters, *P. agardhii* can outcompete other phytoplankton species—including other cyanobacteria—by diminishing the opportunities for

Table 1 Different cyanobacterial functional groups, with their preferable habitats, typical representatives, tolerances, key traits, sensitivities and the possible management actions, are displayed

Group	Habitat	Typical representatives	Tolerances	Key traits	Sensitivities/management action
S_1/S_2 (non-N_2-fixing filaments)	Deep/shallow Turbid mixed layers	***Planktothrix agardhii*** *Arthrospira*	Light deficiency	Efficient light harvesting	Short residence time/ flushing
S_N (filaments)	Warm mixed layers	***Cylindrospermopsis raciborskii*** *Anabaena minutissima*	Light, N deficiency	N_2 fixation Optimal growth rate at elevated temperatures Resting cells	Short residence time/ flushing
H_1/H_2 (filaments)	Small/large Mesotrophic lakes	***Dolichospermum flos-aquae*** *Gleotrichia echinulata*	N, C deficiency	N_2 fixation Buoyancy Resting cells	Light deficiency/artifical mixing P deficiency/control of phosphorus loading
L_O/L_M (colony)	Mesotrophic/ eutrophic Summer epilimnia	*Woronichinia* ***Microcystis***	C deficiency Stratification	Buoyancy	Light deficiency/artificial mixing
R (non-N_2-fixing filaments)	Metalimnia of mesotrophic stratified	***Planktothrix rubescens*** *P.mougeotii*	Light deficiency Strong segregation of light and nutrients	Buoyancy Efficient light harvesting	Physical instability/artificial mixing, stringent nutrient control

In the **S_1/S_2**, **H_1/H_2** and **L_O/L_M** combined groups, several habitat types and typical representatives are enlisted to facilitate the association of each group to certain key traits and possible management actions. The highlighted typical representative in each group is used further in the text to describe how certain key traits are affected by environmental changes and propose certain solutions for the management of their occurrence

light harvesting for those which are less well adapted to light deficiency (Reynolds 2006). Under nutrient-rich conditions, the excess of *P. agardhii* biomass promotes the conditions for its own growth by creating appropriate light-limiting conditions (Reynolds 2006; Scheffer et al. 1997). The occurrence of *P. agardhii* blooms as an exponent of eutrophication in shallow lake ecosystems follows the concept of alternative stable states (Scheffer et al. 1997). At low P concentrations, the dominance of *P. agardhii* is absent, since there are insufficient nutrients to create the turbid conditions on which this cyanobacterium depends. With ongoing eutrophication, the conditions for *P. agardhii* gradually improve, until at a critical *P* value the mixed phytoplankton community collapses and only *P. agardhii* remains. The water is now so turbid that only *P. agardhii* can maintain growth and sustain its population. Upon lake restoration (reduction in P loading), initially nothing will happen, since also the turbid state is stable and maintains its own prolongation, helped for instance by high biomass of benthivorous fish species, like bream which stir up the

sediment, thereby increasing the turbidity too (Lammens et al. 2004; Roozen et al. 2003). A long period of hysteresis may follow (Ibelings et al. 2007). At some point during the restoration process, however, the P concentration becomes too low to support a high *P. agardhii* biomass, in particular when external factors like cold winters break up the bloom (Berger 1975; Scheffer et al. 1997) or restoration measures like biomanipulation are carried out. At this point, the underwater light climate has improved sufficiently to allow a return to a mixed phytoplankton community and *P. agardhii* will disappear. *P. agardhii* has a tendency to show biomodality in its distribution, either it is dominant or it is nearly absent, a hallmark of alternative stable states (Scheffer et al. 1997).

Management actions

Controlling the nutrient input, thus improving the lake's light environment by diminishing turbidity, is the most fundamental solution to avoid the occurrence

of filamentous cyanobacteria with efficient light-harvesting abilities (Van Liere and Walsby 1982). However, several attempts to restore the original phytoplankton community in shallow lakes by reducing the nutrient loading were not always successful, in particular in the short term (Sas and Ahlgren 1989). Increased flushing rates could be effective for the management of *P. agardhii*. Observations from 27 case studies of lakes undergoing restoration (reduction in P loading) in Denmark demonstrated that in cases where the hydraulic retention time was long, lakes recovered more slowly from cyanobacterial dominance than lakes with low retention times (<0.5 years), where the recovery was 10–300 times faster (Jeppesen et al. 1991). This can be explained by the fact that the maximum growth rate of the filamentous *P. agardhii* (as in many cases of several cyanobacterial taxa) is typically ca. only half of the maximum growth rate of green algae ($r = 0.6$ day^{-1} vs. $r = 1.2$ day^{-1}, respectively, calculated by Scheffer et al. 1997 based on Mur et al. 1977). Consequently, longer retention time favors *P. agardhii*, while short retention time may remove it from the system, as *P. agardhii* no longer has the capacity to outcompete fast-growing green algae. Scheffer et al. (1997) prediction model confirmed that *P. agardhii* would be absent independently of the nutrient level if the flushing rate was $\approx 18~\%$ of the lake volume per day. Increased flushing rates along with increased water clarity can reduce hysteresis of lakes dominated by *P. agardhii* and lead to a faster return to a mixed phytoplankton community. Crucial for the long-term restoration of lakes formerly dominated by *P. agardhii* is the return of an abundant macrophyte community which competes for nutrients with the cyanobacterium, prevents sediment re-suspension and provides shelter for large-bodied zooplankton against fish predation (Gulati et al. 2008).

S$_N$: Warm mixed layers—*Cylindrospermopsis raciborskii*

Key traits

According to Reynolds classification (Reynolds 2006), the main representatives of the S$_N$ group proliferate in warm mixed layers. In this paper, we will focus mainly on *C. raciborskii* whose occurrence is expanding. *C. raciborskii* blooms can negatively affect water quality since they can produce toxins such as the neurotoxin saxitoxin (Castro et al. 2004) and the alkaloid hepatotoxin, cylindrospermopsin (Li et al. 2001). The *C. raciborskii* distribution range used to be restricted to tropical and subtropical ecosystems, but since the 1930s, it has progressively colonized more temperate environments, spreading from Greece and Hungary toward higher latitudes by the end of the twentieth century (Padisák 1997). These expanding *C. raciborskii* strains have been reported as not toxic (Fastner et al. 2003; Yilmaz et al. 2008). However, a recent study by Gkelis and Zaoutsos (2014) revealed saxitoxin production in freshwater samples from Greece dominated by *C. raciborskii*. The expansion of *C. raciborskii* is supported by the existence of different physiological strains or ecotypes, which vary in their temperature tolerance with tropical strains to be tolerant in a temperature range of 15 to 35 °C (Chonudomkul et al. 2004).

C. raciborskii occurs mainly in shallow eutrophic waters with relatively high turbidity (Reynolds 2006). It holds common phenotypic traits with *P. agardhii* such as tolerance to continuous mixing and shaded water columns (Stüken et al. 2006). Another similarity is its high affinity for and ability to store phosphorous under limiting conditions (Istvanovics et al. 2000) that allows *C. raciborskii* to proliferate in warm surface mixed layers of stratified systems (Bormans et al. 2004). These shared key traits between *P. agardhii* and *C. raciborskii*, which are also depicted in their similar morphological characteristics, indicate functional equivalence and a probability of occupying comparable niches (Kruk et al. 2010). For example, in eutrophic lakes in Eastern Germany, cyanobacteria assemblages consist mainly of members of the S$_1$ group (Reynolds 2006), but are often accompanied by *C. raciborskii* (Nixdorf et al. 2003). There are specific details, however, which differentiate the niches in which each of these cyanobacterial species proliferate, for example, *C. raciborskii*, has higher light requirements for growth than *P. agardhii* (Briand et al. 2004). Additionally, *C. raciborskii*, as a Nostocales genus, has the capacity to fix atmospheric nitrogen in its heterocysts (Komárek and Mareš 2012).

Key traits under eutrophication and climate change

Experiments under different temperature regimes showed a positive net growth in a wide range of

temperatures from 15 to 35 °C and light intensities ranging from 30 to 400 μmol photons m^{-2} s^{-1} of strains of both tropical and temperate origin (Briand et al. 2004). The colonization of *C. raciborskii* of mid-latitudinal environments hence may be a result of a high adaptability to a range of light and temperature gradients under perpetual environmental change induced by eutrophication and global warming (Briand et al. 2004). The characteristic of N$_2$ fixation promotes its competitive strength under nitrogen-depleted environments, enabling it to effectively compete against other species like *P. agardhii* that is not able to fix nitrogen (Anagnostidis and Komárek 1988). Experiments, however, showed that *C. raciborskii* is capable of dominating over a mixed phytoplankton community of green algae and other cyanobacteria species regardless of N/P stoichiometry (Chislock et al. 2014), which reduces the capability to control its occurrence under eutrophic conditions in freshwater ecosystems. Moreover, *C. raciborskii* has the advantage of forming akinetes (Kaplan-Levy et al. 2010) as an effective means to survive unfavorable periods such as changes in light, nutrients, temperature or desiccation. These akinetes can also capitalize on the excess availability of P in the sediment upon germination (Istvanovics et al. 2000).

Management actions

Controlling the nutrient load of both N and P may be necessary to control the blooms of this harmful cyanobacterium (Chislock et al. 2014). Additionally and similar to the previous group (S$_1$/S$_2$), Reynolds (2006) suggests that problems with *C. raciborskii* can be solved if the retention time in basins is shortened sufficiently under increased flushing rates. In a large impounded tropical river, Bormans et al. (2005) showed that flushing was the only management option to terminate blooms of *C. raciborskii*.

H$_1$/H$_2$: Dinitrogen-fixing nostocaleans— *Dolichospermum flos-aquae* (formerly *Anabaena flos-aquae*)

Key traits

In the H$_1$/H$_2$ group, we have dinitrogen-fixing nostocaleans that occur mainly in small or large

mesotrophic lakes (Table 1). Here, we will focus on *D. flos-aquae* in order to show how the key traits that characterize the H$_1$/H$_2$ group support their tolerance to limiting nitrogen availability and how we can exploit their sensitivities to eliminate their presence in freshwater ecosystems. *D. flos-aquae* is a filamentous cyanobacterium that can be highly toxic when present in water resources (Agnihotri 2013) producing harmful neurotoxins such as anatoxin-a, anatoxin-a(s) and homoanatoxin-a (Gallon et al. 1990). *D. flos-aquae* is a good competitor under low nitrogen supplies as it can fix nitrogen while it can escape poor light conditions by regulating its buoyancy (Kinsman et al. 1991; Reynolds 2006).

Nitrogen fixation is an energetically costly process that depends on light as an energy source. The rates of N$_2$ fixation increase with increasing light levels (Agawin et al. 2007). Low N/P ratios stimulate heterocyst development (Agawin et al. 2007), resulting in an increase in the N-fixers' biomass either in mesocosm experiments (Levine and Schindler 1999; Vrede et al. 2009) or in whole-lake experiments (Schindler et al. 2008). Experimental studies also point out that promotion of nitrogen fixers occurs only when sufficient light is provided (de Tezanos Pinto and Litchman 2010a). Light regime has a primary significance for the success of *D. flos-aquae* as under low photon fluxes N/P ratios appear not to have a significant effect on its abundance (de Tezanos Pinto and Litchman 2010a). Under low light intensities, which stimulate gas vesicle production (Kinsman et al. 1991), *D. flos-aquae* may take advantage of its gas vesicles to regulate its buoyancy, float up and in this way may manage to enhance access to light and sustain its biomass (Carey et al. 2012).

Key traits under eutrophication and climate change

Anticipated changes in the environment can stimulate the occurrence of *D. flos-aquae* in different ways. Increased temperatures induce stronger stratification and shallower mixing depths, resulting in increased light availability for floating cyanobacteria like *D. flos-aquae*, which would benefit N$_2$ fixation under low N availability. High temperatures also have a direct effect on optimizing N$_2$ fixation by enhancing the rate of gas diffusion into the heterocyst (Bauersachs et al. 2014). Staal et al. (2003) found that Q10 (acceleration of a process over a 10 °C step, generally 10–20 °C)

values for N_2 fixation of heterocystous strains of *Anabaena sp.* were approximately equal to cyanobacterial growth rate responses to temperature ($Q10 \geq 1.8$, Reynolds 2006).

Management actions

A potential remedy against blooms of N_2-fixing cyanobacteria would be to reduce light availability. Deep mixing can have a negative effect on the growth of *D. flos-aquae* and its capacity to fix nitrogen, as it forces the population down to poorly illuminated waters with low energy supply. In general, N_2 fixation is also restrained through the availability of phosphorus and micronutrients (molybdenum, iron) as the N_2-fixing enzyme, nitrogenase, requires high levels of these nutrients to operate (Vitousek et al. 2002). Hence, for several N_2 fixers, Schindler (1977) puts forward that P is the ultimate limiting factor in freshwater ecosystems of moderate to high productivity, so that control of P could effectively control H_1/H_2 (see, however, Chislock et al. 2014 who showed that stoichiometric manipulation of N and P will not be enough as experiments on *C. raciborskii* showed its dominance under high or low N/P ratios). Reynolds (2006) in this case also points out that the H_1/H_2 group does not perform well under low phosphorus concentrations.

Lo/L_M: Summer epilimnia—*Microcystis aeruginosa*

Key traits

Lo/L_M are encountered when lake summer epilimnia are formed in mesotrophic and eutrophic lakes (Table 1). Our main concern here will be the genus *Microcystis*. *Microcystis* is a cosmopolitan genus which can generate dense cell accumulations (scums) on the surface of freshwater ecosystems, threatening human and ecosystem health (Visser et al. 2005). Several strains of *Microcystis* spp. are toxigenic producing a group of cyclic peptide hepatotoxins called microcystins and consist a risk for both public health and ecosystems (Carmichael 1997). *Microcystis* spp. forms large colonies that put it at a disadvantage under nutrient limited conditions as its low surface area-to-volume ratio decelerates nutrient

uptake rates (Reynolds 1997). Large colonies will move faster compared with smaller colonies or single filaments, following Stokes' law (Smayda 1971). *Microcystis* has been referred to as the champion of buoyancy regulation. *Microcystis* efficiently regulates its buoyancy by varying its dense cellular constituents (mainly sugars) on a diel timescale, and buoyant colonies float up rapidly during periods of (partial) water column stability (Ibelings et al. 1991). Therefore, forming large colonies that can float fast is a key advantage for *Microcystis* (Ibelings et al. 1991). In experiments, *M. aeruginosa* was able to migrate 12 m within 2 h to gain access to both light and nutrients, defeating any density barriers (Ganf and Oliver 1982). Observations in the Dutch Lake Vinkeveen have demonstrated (Ibelings et al. 1991) that *Microcystis* spp. fast flotation velocity (Walsby 1991) allows it to efficiently track the near-surface mixed layer (Humphries and Lyne 1988) floating up until it reaches the well-mixed layer near the lake surface where even large colonies will remain entrained in turbulent flow.

Key traits under eutrophication and climate change

Increased temperatures are positively related to *M. aeruginosa*'s growth rate as it reaches a maximum replication rate at 28 °C while its Q10—here the increase in growth rate with a 10 °C increase in temperature—reputedly is close to 9.6, one of the highest values recorded in prokaryotic and eukaryotic phytoplankton species (Reynolds 2006; Carey et al. 2012). However, Lürling et al. (2013) demonstrated experimentally that the optimum growth temperature for several cyanobacterial and green algal taxa was not significantly different. Although Lürling et al. (2013) suggest that *M. aeruginosa* might not benefit from higher water temperatures, Paerl and Huisman (2009) do support the notion that *M. aeruginosa*'s blooms will be promoted albeit through the indirect effects of climate warming. Increased temperatures lead to intensified density differences enhancing lake stratification. When the stratification is well developed, shallow wind-induced mixing in the surface layer cannot be transferred to deeper layers, denying other phytoplankton the opportunity to become entrained in turbulent flow. Under stable stratification and reduced turbulence, *M. aeruginosa* colonies will be larger and their buoyancy will be further enhanced during vertical migration cycles (O'Brien et al. 2004).

Consequently, *M. aeruginosa's* ability to efficiently control its movement offers a clear advantage over non-migrating phytoplankton species under the expected prolonged and enhanced stratification (Carey et al. 2012; Paerl and Huisman 2009).

Management actions

Reynolds (2006) proposes a prolonged deep mixing regime in order to control the occurrence of *M. aeruginosa* (Table 1). The management of *Microcystis* in the Dutch Lake Nieuwe Meer showed that artificial mixing using bubble plumes can effectively prevent nuisance blooms and promote a mixed community of flagellates, green algae and diatoms (Visser et al. 1996). Non-buoyant algae were favored since their sedimentation rates were reduced due to the artificial mixing, while the turbulent flow diminished the advantage of *M. aeruginosa* to float up into the illuminated near-surface mixed layer (Visser et al. 1996). Under mixing, cells face rapid changes in light regime and competition leans toward those eukaryotic competitors that are better adapted to fluctuating irradiance levels compared to *M. aeruginosa* (Ibelings et al. 1994).

R: Metalimnia in stratified lakes—*Planktothrix rubescens*

Key traits

The representatives of group **R** (Table 1) are encountered in the metalimnion of mesotrophic, stratified lakes (Reynolds 2006). *P. rubescens* is a filamentous cyanobacterium that may produce the hepatotoxin microcystin (Anagnostidis and Komárek 1988). It contains gas vesicles that allow it to adjust its buoyancy and regulate its position in the water column. In contrast to *Microcystis*, however, it positions its populations away from the saturated irradiance levels at the lake surface (Jacquet et al. 2005). It belongs to the same genus as *P. agardhii* from the S_1/S_2 group, and both species are able to tolerate low light intensities as both share the same slender filamentous form and auxiliary pigmentation (Reynolds 1997). Nevertheless, the niches of the two congeners are clearly different. Whereas *P. agardhii* prefers a shady (turbid) environment, *P. rubescens*

requires a relatively clear epilimnion. *P. rubescens* forms metalimnetic layers in deep, stratified meso-eutrophic lakes where it can completely monopolize resources and dominate the phytoplankton community (Anneville et al. 2004). At metalimnetic depths, the light quantity and light quality are different compared to the upper mixed layers and *P. rubescens* is well adapted to these light conditions due to the abundance of the red pigment phycoerythrin.

The morphology of gas vesicles has evolved to withstand the combined pressures in the lake environment (Walsby 1994). Strains of *P. rubescens* have narrow gas vesicles (diameter = 50 nm) with critical collapse pressure (pc) ≈ 1.1 MPa compared to *M. aeruginosa* ($d = 65$ nm, pc ≈ 0.85 MPa) as response to withstand increased hydrostatic pressure that comes with increased depth (Visser et al. 2005). The *P. rubescens* gas vesicles will survive during deep winter mixing, and cells maintain their buoyancy (Carey et al. 2012). Moreover, following Stokes' law in non-turbulent conditions, filaments with a small diameter will have a low sinking or flotation velocity, compared to large colony-forming taxa (Walsby 2005) and will find it easier to maintain position in the metalimnion. The intimate interactions between carbohydrate accumulation and gas vesicle-mediated buoyancy will support close-to-neutral buoyancy and will maintain filaments at a given depth (Walsby et al. 2004). Overall, *P. rubescens* is able to adjust the depth of its stratifying population in response to changes in the underwater light regime and will take up different positions in the metalimnion if this is to its advantage (Jacquet et al. 2005).

Key traits under eutrophication and climate change

P. rubescens is present in high biomass during summer, when the phosphorus concentrations are very low in the epilimnion, but still remain available in deeper layers of lakes (Anneville et al. 2002). *P. rubescens* can even keep developing during autumn when there is lower irradiance due to increased mixing, forcing the thermocline to greater depth (Anneville et al. 2004). *P. rubescens* can be successful under different trophic states of the same lake; this has been observed in Lake Zurich (Switzerland) where *P. rubescens* has been found in phytoplankton assemblages during both the eutrophic and the meso-eutrophic stages of the lake (Anneville et al. 2004).

In Lake Bourget (France), however, the long-term dynamics show a different pattern. *P. rubescens* was absent prior to eutrophication in the 1950s, while also the very nutrient-rich conditions during the peak of the eutrophication prevented proliferation of this filamentous species. *P. rubescens* came to dominate Lake Bourget in the mid-1990s when lake restoration measures began to take hold. Lake restoration has been successful, even to the point that since 2009 *P. rubescens* once more is absent from the lake. Hence, the relationship between trophic state and proliferation of *P. rubescens* follows a hump-shaped pattern, where the peak of the hump is positioned at mesotrophic to meso-eutrophic conditions (Dokulil and Teubner 2012).

Recent studies show the importance of the seasonal effects of climate change on the deep, meso-eutrophic lakes in the peri-alpine region where *P. rubescens* typically dominates (Anneville et al. 2015; Posch et al. 2012). Contrary to the common belief that blooms prefer hot summers (Jöhnk et al. 2008), extremely warm summers (like the one in 2003) do not promote blooms of *P. rubescens*, and they may reduce its population size. Apparently, *P. rubescens* does not benefit from extremely long and stable stratification during heat wave summers, despite the ongoing depletion of epilimnetic nutrient concentrations. Warm conditions in autumn and winter, however, do promote *P. rubescens* in the following year, indicating the vital role of carrying on a large enough inoculum for growth through the winter to the next spring period.

Management actions

The return of *P. rubescens* in Lake Bourget in the mid-1990s upon a return to mesotrophic conditions is attributed to increased transparency following the restriction of other phytoplankton species under increasingly reduced phosphorus availability (Jacquet et al. 2005). Ernst et al. (2009) suggested that the effects of climate change strengthen the dominance of *P. rubescens* in peri-alpine lakes that undergo re-oligotrophication, because this cyanobacterium can take advantage of the earlier onset of stratification. Reduced mixing in warmer winters (incomplete overturn of the water column) will stimulate survival of intact gas vesicles in *P. rubescens* (Walsby et al. 1998), aiding to achieve a large size of the inoculum. For these reasons, Reynolds suggested to alter the stability of the water column as an effective means to disrupt the development of *P. rubescens* (Reynolds 2006).

Lake managers worldwide, for instance in the Netherlands, are aware of the increasing risks of toxic cyanobacteria during heat waves, resulting in lakes being closed for recreation on an extensive scale (Ibelings et al. 2014). In contrast to the peri-alpine region, however, lakes in the Netherlands tend to be dominated by cyanobacteria from the ##L_O/L_M group. These "subtle" differences between effects of warming in summer versus winter upon different functional groups—**R** versus L_O/L_M—underline once more the necessity to study and control cyanobacterial blooms upon the right—ecological—basis. Cyanobacteria with different key traits will respond differently to changes in the environment and require a different management approach.

Conclusions and research perspectives

Cyanobacterial blooms are still a major problem in freshwater ecosystems in spite of major nutrient reductions over the last 40 years. Lake restoration has had mixed success in controlling their development. The anticipated changes of our climate have the capacity to worsen the problem, demanding appropriate and timely measures from lake managers. In this review, we demonstrate how management actions should be tailored depending on the dominant cyanobacterial functional group. Identifying the key traits of dominant cyanobacteria and the environmental conditions under which these traits succeed can reveal the Achilles heel of cyanobacterial functional groups and provide lake managers with the most appropriate tools for their effective management and control. A comprehensive view of the many adaptive strategies of cyanobacteria to a wide range of environmental conditions is essential as controlling one species has also the potential to let another (maybe even more problematic) species proliferate. This knowledge on the cyanobacterial key traits should be more incorporated in various models developed and used to predict bloom occurrences. Yet, crucially all taxa ultimately can and should be controlled by managing the external and internal nutrient loading of lakes. This special issue in Aquatic Ecology presents the state of the art in cyanobacterial bloom

management and control, continuously keeping the key ecophysiological traits of the culprits in mind.

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