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SPECIAL REVIEW

Understanding cyanobacteria-zooplankton interactions in a more eutrophic world

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SUMMARY

1. We review and update recent observations of cyanobacteria–zooplankton interactions, identify theoretical and methodological limitations and evaluate approaches necessary for understanding the effects of increasing cyanobacterial blooms on plankton dynamics.
2. The emphasis on oversimplified studies using large-bodied *Daphnia* species, not previously exposed to cyanobacteria, has limited our understanding of how the plankton responds to proliferating blooms. This overlooks the great diversity in zooplankton traits, and the adaptability of planktonic grazers, that enables them to deal with toxic prey.
3. Under increasing temperature and nutrient loading, the zooplankton will be subjected to increasingly intense selection pressure to tolerate cyanobacteria. Short zooplankton generation times suggest that increased blooms may select for the rapid evolution of behavioural and physiological traits that improve tolerance.
4. As eutrophication intensifies, should we expect physiologically tolerant zooplankton that may be able to control blooms, or be concerned with the effects of selective grazers in stabilising blooms?
5. We conclude that the increasing frequency, duration and intensity of blooms will select for better adapted zooplankton that coexist with, rather than control, cyanobacteria. Future evaluations of cyanobacteria–zooplankton interactions should consider that increasing exposure to blooms induces phenotypic and genotypic traits improving zooplankton tolerance. Equally important will be studies of the ecophysiology of zooplankton species that coexist with prolonged blooms, rather than those of a few large-bodied generalist cladocerans.
6. Since cyanobacteria produce more than one toxic or inhibitory metabolite, the unsystematic designation of toxicity based on single well-identified compounds (e.g. microcystin) should be revised.
7. Overall, the coevolutionary interaction between cyanobacterial defences and zooplankton grazer responses emerges as a critical but understudied regulator of bloom dynamics.

Keywords: ecosystem – level of organisation, eutrophication – applied issues, fresh waters – habitat, nuisance algae – applied issues, other species interactions – process/approach/methods, plankton – taxonomic group/assemblage

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Introduction

As cultural eutrophication has become one of the most apparent human changes to aquatic systems, its symptoms have been revealed as the chief water quality concern for inland and coastal waters (Karjalainen *et al.*, 2007; Smith & Schindler, 2009). The classic sign of eutrophication in freshwater and estuarine systems is blooms of cyanobacteria such as *Microcystis*, *Cylindrospermopsis*, *Anabaena*, *Planktothrix*, *Aphanizomenon* and *Nodularia*, which dominate the phytoplankton community and disrupt food-web processes due to their high abundance, toxicity and reduced food quality for grazers (Carmichael, 1991; Wiegand & Pflugmacher, 2005; Paerl & Paul, 2012). Few doubt that global changes will lead to intensified cyanobacterial dominance of aquatic systems (Paerl & Huisman, 2009). Remarkably, despite its importance for resource management and regardless of the very many laboratory and field observations, our understanding of the effects of cyanobacteria on plankton dynamics remains inadequate and contradictory (Twombly, Clancy & Burns, 1998; Wilson, Sarnelle & Tillmanns, 2006; Sarnelle, 2007).

Compared with other phytoplankton, cyanobacteria have three major attributes as food organisms that can reduce zooplankton growth. The production of toxic metabolites, including hepato- or neurotoxins, and various other less known compounds causes lethal and sublethal effects when ingested by zooplankton (Leflaive & Ten-Hage, 2007). Cyanobacteria also limit zooplankton fitness because they are deficient in sterols and the long-chained polyunsaturated fatty acids (PUFAs), vital for regulating cell function in animals (Gulati & Demott, 1997; Müller-Navarra *et al.*, 2000). Finally, the aggregation of cyanobacterial cells into large, inedible colonies or filaments provides a grazer refuge, and moreover, filaments can inhibit grazing by large daphniids by clogging the filtration apparatus (Gliwicz & Lampert, 1990; DeMott, Gulati & Van Donk, 2001). Overall, these attributes make cyanobacteria an inedible or poor quality food, which can effectively function as defences against zooplankton grazing with significant yet largely unknown ecoevolutionary implications.

Despite numerous references mentioning the mass occurrence of cyanobacteria or surface scums, there is no universal definition of a 'bloom'. As in any population, cyanobacteria grow when accumulation of their biomass exceeds losses through biological and physical processes (Mitra & Flynn, 2006). We use the term 'bloom' for conditions when cyanobacteria are >50% of total phytoplankton biomass and their abundance is $>10^4$ cells mL^{-1} in ecologically representative water samples. Significant negative effects on zooplankton and water quality generally occur above this concentration (Falconer *et al.*, 1999). Ecologically, blooms indicate the build-up of inedible phytoplankton biomass that inhibits the transfer of primary production energy to zooplankton grazers (Müller-Navarra *et al.*, 2000).

The relatively weak coupling between primary producers and zooplankton grazers during blooms explains why attempts at biomanipulation by increasing the zooplankton have been relatively ineffective in controlling blooms (Boon *et al.*, 1994; Scheffer & Rinaldi, 2000; Xie & Liu, 2001; Rondel *et al.*, 2008). When the phytoplankton is edible (i.e. strong zooplankton and phytoplankton coupling), zooplanktivorous fish control phytoplankton abundance through cascading effects on herbivore abundance (Tessier & Woodruff, 2002). In contrast, during blooms of inedible phytoplankton, cascading effects on cyanobacterial bloom development are rare even when zooplankton abundance is unrestricted by fish predation (Mitra & Flynn, 2006; Lacerot *et al.*, 2013). In fact, the quality and palatability of autotrophs as food may be more important than fish predation in determining the degree of zooplankton–phytoplankton coupling (Dickman *et al.*, 2008). This is likely to explain why an increasing predominance of inedible cyanobacteria inhibits cascading effects from zooplanktivorous fish to phytoplankton biomass (Rondel *et al.*, 2008). However, large generalist grazers such as *Daphnia* have been shown temporarily to prevent cyanobacterial blooms in lakes with suppressed zooplanktivorous fish (Elser *et al.*, 2000). Similarly, *Daphnia pulicaria* in fishless enclosures and ponds is able temporarily to control cyanobacterial biomass (Sarnelle, 2007; Sarnelle, Gustafsson & Hansson, 2010). Hence, while the inhibitory role of defences against grazers on trophic cascades is well established, the latter examples show that cascades in bloom-dominated systems may still occur under some circumstances.

The relationship between cyanobacterial defences and zooplankton responses is emerging as a critical but understudied process that regulates the trophic interactions of blooms. Much previous research has focussed on the negative effects on zooplankton populations of the low food quality or toxicity of cyanobacteria (Wilson *et al.*, 2006; Tillmanns *et al.*, 2008). However, conventional predictions that cyanobacterial blooms should therefore reduce zooplankton fitness do not explain the increasing observations of the persistent coexistence in nature of both groups (Bouvy, Pagano & Troussellier, 2001; Panosso *et al.*, 2003; Sarnelle, 2007; Ka *et al.*, 2012). Further, a striking variation in observed zooplankton responses has prevented the generalisation of species interactions to predict plankton dynamics (Wilson *et al.*, 2006). In this review, we identify the major limitations in the field of cyanobacteria–zooplankton interactions, update and evaluate the current knowledge in the light of recent observations and, lastly, highlight methods necessary for overcoming the present hurdles to predict accurately bloom effects on plankton dynamics.

Current limitations

Perhaps the most striking factor that limits predictions is the extrapolation of experimental results obtained from clones of a few species of *Daphnia* for understanding zooplankton responses to cyanobacteria. Cyanobacteria–zooplankton interactions have mainly been studied using large *Daphnia* as the model grazer (Wilson *et al.*, 2006; Tillmanns *et al.*, 2008). There is good reason for the emphasis on large-bodied *Daphnia* because they are efficient grazers of particles of a wide size range and thus represent the zooplankton type with the highest potential to control blooms. Indeed, *Daphnia* species can prevent blooms, especially if their abundance is high enough before cyanobacteria begin to dominate the phytoplankton (Sarnelle, 2007). However, such examples are rare, and most forecasts predict that blooms will shift the zooplankton community from *Daphnia* to other taxa, such as copepods and smaller cladocerans (Fulton & Paerl, 1987; Hansson *et al.*, 2007).

While predictions based on our knowledge of *Daphnia* are important for the initial effect of blooms where *Daphnia* is dominant, they are less applicable for the plankton dynamics of more persistent blooms, which are characterised by the better adapted zooplankton that coexist and interact with cyanobacteria (DeMott & Moxter, 1991; Kirk & Gilbert, 1992; Kurmayer, Christiansen & Chorus, 2003; Ka *et al.*, 2012). Indeed, in places where cyanobacterial blooms persist, the zooplankton biomass is often dominated by copepods and smaller cladocerans (Haney, 1987; Bouvy *et al.*, 2001; Koski *et al.*, 2002; Panosso *et al.*, 2003; Work & Havens, 2003; Rondel *et al.*, 2008; Wang *et al.*, 2010). Focussing merely on a few large *Daphnia* species ignores plankton dynamics in systems subject to blooms that are dominated by better adapted zooplankton species. Consequently, the interaction of copepods and smaller cladocerans with cyanobacteria remains largely unexplored.

Another significant research bias emerges as we recognise how most studies have observed the effects of cyanobacteria on zooplankton over time periods that are relatively short compared with the duration of blooms. A notable series of recent observations shows that tolerance to cyanobacterial toxins is higher for zooplankton previously exposed to cyanobacteria (Gustafsson, Rengefors & Hansson, 2005; Sarnelle & Wilson, 2005), indicating that prolonged blooms may result in more tolerant herbivores. Hence, predictions based on the responses of ‘naive’ zooplankton have become increasingly irrelevant because climate change and human population growth are expected to increase the abundance and duration of cyanobacterial blooms (Paerl & Huisman, 2009; Kosten *et al.*, 2012; Paerl & Paul, 2012), which is likely to induce adaptive traits within zooplankton species (Kirk & Gilbert, 1992).

A third topic, which is almost entirely overlooked, is the effect of zooplankton grazing on cyanobacterial defences and *vice versa*. The relationship between cyanobacteria and zooplankton may be strongly characterised by coevolutionary dynamics between the grazer and its food, where both actors are responding to maximise their own fitness. The premise of this interaction is an evolutionary arms race, in which the zooplankton adapts for higher tolerance (Hairston *et al.*, 2001) while cyanobacteria develop grazing defences (toxicity, bad taste cues and morphology; Jang *et al.*, 2003; Jang, Jung & Takamura, 2007). Despite this two-way interaction between the groups, research has mainly focussed on the effects of cyanobacteria on zooplankton, whereas little is known about the reciprocal response of cyanobacterial defences to zooplankton grazing.

The ecology and rapid evolution of induced traits selected by cyanobacteria–zooplankton interactions will probably shape the structure and function of planktonic systems in a more eutrophic world. As blooms become even more widespread, results from previous research raise the guiding questions for plankton ecologists.

1. What is the nature of and variability in zooplankton adaptations to cyanobacteria?
2. How do better adapted zooplankton interact with cyanobacteria?
3. How do cyanobacteria adapt to zooplankton grazers?
4. What are the plankton dynamics during longer blooms?
5. What approaches are necessary to understand the coevolutionary dynamics shaping cyanobacteria–zooplankton interactions?

Below, we identify and summarise key attributes relevant to the cyanobacteria–zooplankton interaction to address each topic above. For the last, we suggest future research goals by categorising these attributes into simple and easily testable predictions for identifying the drivers of plankton dynamics in systems dominated by blooms.

The nature of and variability of zooplankton adaptations to cyanobacteria

Zooplankters have two distinct adaptations to minimise the negative effects of cyanobacteria. In general, they either restrict the ingestion of toxic cells via feeding adaptations (i.e. selective feeding) or increase their physiological tolerance of ingested toxic cells via more efficient detoxification mechanisms (Pflugmacher *et al.*, 1998; Gustafsson *et al.*, 2005; Sarnelle & Wilson, 2005). Hence, ingestion and tolerance (and their fitness costs) are the principal metrics of zooplankton adaptations to cyanobacteria. While it is accepted that cyanobacteria are a poor food source reducing zooplankton fitness, tolerance of cyanobacteria and their ingestion by zooplankton are remarkably variable (Haney, 1987; Twombly *et al.*, 1998; Kumar, 2003; Ger *et al.*, 2010b).

Both among- and within-species differences in zooplankton response to different strains of cyanobacteria have made generalisations about plankton interactions difficult (Twombly *et al.*, 1998; DeMott, 1999; Koski *et al.*, 2002; Sarnelle & Wilson, 2005). Even clones of the same zooplankton species can have different tolerance to a cyanobacterium, causing geographical differences in the response of zooplankton species to cyanobacteria across space or time (Wilson & Hay, 2007; Ferrao *et al.*, 2008; Ger, Teh & Goldman, 2009). Such intraspecific variation in tolerance represents a high potential for microevolutionary responses to increased cyanobacterial abundance. Indeed, exposure to cyanobacteria can select for improved zooplankton tolerance traits that can be transferred to future generations (Gustafsson *et al.*, 2005). However, the nature of these traits depends on the duration of exposure. While exposure across longer timescales can result in interspecific variation (macroevolution), shorter periods of exposure result in intraspecific variability among populations (microevolution), and exposure during the lifetime of the organism can induce physiological or behavioural responses. Distinguishing among these adaptations is fundamental for understanding zooplankton responses to increasing blooms. The examples below summarise current evidence for the different zooplankton adaptations among species, populations and individual organisms.

Macroevolutionary adaptations to cyanobacteria (interspecific differences)

These refer to the different adaptations driven by selection over macroevolutionary timescales, such as selective versus generalist grazing apparatus among zooplankton taxa and the evolution of metabolic pathways involved in the detoxification of ingested cyanobacterial toxins. Copepods show a high degree of feeding selection by maximising the ingestion of the most nutritious food from a mixture of particles using chemosensory detection to differentiate the size, nutrition and digestibility of encountered particles (DeMott, 1989; Kleppel, 1993; Tackx *et al.*, 2003; Tirelli & Mayzaud, 2005). When cyanobacteria are encountered, copepods use different cyanobacterial secondary metabolites (such as microcystin, lipopolysaccharides and unidentified lipophylic compounds) as detection cues to avoid ingestion (Kurmayer & Juttner, 1999; Engstrom *et al.*, 2000; Ger, Panosso & Lurling, 2011). Consequently, selective feeding usually allows copepods uninhibited feeding on alternative food in the presence of toxic cyanobacteria, resulting in the grazer coexisting with blooms (Bouvy *et al.*, 2000; Koski *et al.*, 2002). Nevertheless, species-specific differences exist in the detection cues (Kurmayer & Juttner, 1999), the efficiency of selective feeding (Engstrom *et al.*, 2000) and the correspondence between cues and toxins (Ger *et al.*, 2010a,b; Hong *et al.*, 2012). Thus, although a highly effective adaptation in minimising the ingestion of toxins, selective feeding behaviour is not perfect. Further, depending on the type of toxin, even a few ingested cyanobacterial cells can cause complete feeding inhibition or mortality in copepods (Ger *et al.*, 2010a; Hong *et al.*, 2012).

In contrast, cladocerans are generalist, relatively non-selective feeders that tend to ingest food particles in the same ratio as they are encountered (Kirk & Gilbert, 1992). Large cladocerans avoid ingesting toxic cyanobacteria by the total rejection of all the food particles accumulated in the feeding apparatus when toxicity cues are detected. When cyanobacteria become abundant, cladoceran ingestion rates generally decline or are inhibited altogether, preventing energy intake and reducing fitness (Rohrlack, Henning & Kohl, 1999; Ghadouani *et al.*, 2004; Rohrlack *et al.*, 2005; Soares *et al.*, 2009). Feeding inhibition, such as selective feeding, is controlled by detection cues such as cyanobacterial toxins (Kurmayer & Juttner, 1999) and may result in positive selection for 'good food' in some cladocerans over short-term exposure to cyanobacteria (Kirk & Gilbert, 1992; Tillmanns, Burton & Pick, 2011). Nevertheless, feeding inhibition only serves as a temporary relief, and the fitness of cladocerans (especially large *Daphnia*) decreases over time, either because of reduced energy intake or eventual ingestion of toxic cyanobacterial cells, or both (Lurling, 2003; Ghadouani *et al.*, 2004; Soares *et al.*, 2009). Physical inhibition of the cladoceran feeding apparatus by cyanobacterial filaments can also occur (DeMott *et al.*, 2001). Unlike copepods, the main problem faced by large daphniids is their limited ability to handle individual food particles. Consequently, the cost of avoiding cyanobacteria is reduced feeding on better quality foods during blooms.

A trade-off between the two strategies emerges over evolutionary timescales (>100 generations) where the physiological tolerance of a zooplankton species to ingested cyanobacterial toxins becomes linked to its toxin exposure history (DeMott & Moxter, 1991; DeMott, Zhang & Carmichael, 1991). Generally, species that avoid ingestion by selective feeding are less exposed to, and therefore less tolerant to, cyanobacterial toxins, while generalist grazers are more exposed but also more tolerant to the toxins (Pflugmacher *et al.*, 1998; Kurmayer & Juttner, 1999; Ger *et al.*, 2009). However, some zooplankton may be both selective feeders and have a relatively high tolerance of ingested toxins (DeMott & Moxter, 1991; Reinikainen *et al.*, 2002; Kumar, 2003), meaning that high feeding selectivity does not necessarily imply low tolerance. Regardless, previous exposure to cyanobacteria over evolutionary timescales has probably selected for the improved efficiency of selective feeding and/or detoxification (Kirk & Gilbert, 1992; Schwarzenberger, Kuster & Elert, 2012).

Over the past decade, a remarkable series of studies has highlighted how previous exposure to cyanobacteria can improve zooplankton tolerance across even shorter periods (<10 generations) within taxa (Gustafsson & Hansson, 2004; Gustafsson *et al.*, 2005; Sarnelle *et al.*, 2010). However, we are only beginning to understand the role of this short-term previous exposure as a mechanism that regulates zooplankton adaptations to cyanobacteria. At this point, it is important to distinguish between adaptations based on natural selection (e.g. more tolerant genotypes) from those based on individual acclimation (phenotypic plasticity).

Microevolutionary adaptive responses (genotypic changes among or within populations)

The evolution of tolerant genotypes (e.g. with detoxification genes) requires several generations of exposure, although the fast reproductive rates of zooplankton means that genetic changes can be expected within a few years (Dam, 2013). Initial evidence for this came from the positive relationship between eutrophication and the tolerance of *Daphnia galeata* to cyanobacteria, using individuals raised from the diapaused eggs deposited in sediments of Lake Constance with a gradient in eutrophication history (Hairston *et al.*, 2001). These results are thought to be due to the natural selection of tolerant genotypes between different clones. Similar correlations between past exposure to cyanobacteria and higher tolerance or fitness come from other natural observations (Sarnelle *et al.*, 2010) and from reports of tolerant ‘super *Daphnia*’ clones, from lakes with >80 years of eutrophication history, that are able to graze down *Microcystis* blooms (Chislock *et al.*, 2013). Such reports hint that microevolutionary dynamics can result in zooplankton adaptations which subsequently feedback to trophic interactions.

Induced physiological or behavioural adaptations (phenotypic changes)

In contrast to genotypic selection, phenotypic acclimation refers to inducible physiological or grazing responses that occur over the lifetime of an individual. Evidence for induced acclimation came from observations indicating that previous exposure to cyanobacteria improved the fitness of *Daphnia magna* upon further exposure (Gustafsson & Hansson, 2004) and that smaller cladocerans such as *Moina* and *Ceriodaphnia* may develop stronger tolerance to cyanobacteria after previous exposure compared with larger *Daphnia* (Guo & Xie, 2006). A follow-up study confirmed that improved tolerance in *D. magna* after previous cyanobacteria exposure was an inducible response developed over the lifetime of the individual and, further, that this trait could be transferred to offspring via maternal effects (Gustafsson *et al.*, 2005).

Another study showed how a 5-day exposure to cyanobacteria enhanced the feeding selectivity for ‘good food’ in the calanoid copepod *Eudiaptomus gracilis* (Ger *et al.*, 2011). Clearly, induced responses to short-term cyanobacteria exposure can improve the tolerance traits of individual zooplankton and may be common in nature.

Overall, the existence of tolerant zooplankton clones is remarkable, but how zooplankton improve tolerance or why such clones are not more prevalent is still unknown (Wilson & Hay, 2007; Ferrao *et al.*, 2008). One likely explanation is that tolerance traits do not necessarily increase fitness, because of their metabolic cost. For example, the copepod *Boeckella* had the same fitness when given a *Cryptomonas* (good food) versus a mixed diet with cyanobacteria (bad food; Twombly *et al.*, 1998). Copepods were able to increase reproductive output when exposed to cyanobacteria, but they matured slower (relative to the nutritious diet), resulting in the same fitness for both conditions. These results reflect trade-offs caused by the cost of tolerance adaptations. Admittedly, information regarding the fitness cost of zooplankton adaptations is scarce. However, its variability across species, populations and individuals is critical in determining how adaptive a trait is. A useful method for evaluating the cost of tolerance traits is to compare the fitness of zooplankton across diets with and without cyanobacteria (Dam, 2013). The cost of an adaptation is evident if there is a reduction in fitness when the cyanobacteria are removed from the diet. Moreover, differences in the slope of reaction norms between two zooplankters can be used to distinguish genotypic differences from phenotypic plasticity (Dam, 2013).

Collectively, these recent observations provide insights into the confusing range of inter-and intraspecific variations in zooplankton adaptations to cyanobacteria that have been reported previously (Haney, 1987; Twombly *et al.*, 1998; Tillmanns *et al.*, 2008). Comparing the response of zooplankton using clones with unspecified exposure history and across relatively short time periods has disregarded the induced and microevolutionary adaptations of the studied organisms and is likely to have caused many of the contradictory results. Future studies should therefore avoid the use of zooplankton of unknown origin, because tolerance and feeding behaviour depend on both the geographical and temporal variability in exposure history to cyanobacteria (Wilson & Hay, 2007; Tillmanns *et al.*, 2011). A better approach to understanding zooplankton responses would be to focus on the relationship between previous exposure, grazing and tolerance to cyanobacteria. The positive effects of adaptation to cyanobacteria exposure suggest that longer blooms (i) shift the zooplankton community to more adapted species (Hansson *et al.*, 2007), (ii) select for better adapted genotypes within each zooplankton species (Dam, 2013) and (iii) promote induced physiological or behavioural traits within the lifetime of individual zooplankton (Schwarzenberger *et al.*, 2012).

How do better adapted zooplankton interact with cyanobacteria?

Under increasing temperature and nutrient loading, the zooplankton will be subject to increasingly intense selection pressure to tolerate cyanobacteria (Paerl & Huisman, 2009; Brookes & Carey, 2011; Kosten *et al.*, 2012). Physiological tolerance (detoxification pathways) and selective avoidance stand out as the key traits that zooplankton rely on to improve their fitness in the face of cyanobacterial blooms (Kirk & Gilbert, 1992; Pflugmacher *et al.*, 1998; Kurmayer & Juttner, 1999). Under more eutrophic conditions, selection would be to improve tolerance-enhancing traits and to reduce their metabolic costs. An improved efficiency in these traits (i.e. the fitness costs less than the benefit) could improve zooplankton fitness when exposed to the same toxic cyanobacteria. As such, the nature of these adaptations will probably control whether zooplankton will (i) graze and eliminate blooms, or (ii) coexist with blooms.

Zooplankton adaptations resulting in grazing on cyanobacteria

Zooplankton control of blooms is possible if the benefit of ingesting significant amounts of cyanobacteria is greater than the cost and, thus, depends on the ability of grazers to ingest and reproduce on a cyanobacterial diet. The point of biomanipulation is to increase zooplankton biomass by controlling predation by zooplanktivorous fish, with the assumption that zooplankton will graze on cyanobacteria. Thus, reducing zooplanktivory is not expected to result in zooplankton control of established blooms unless there are large-bodied generalist herbivores (such as *Daphnia*) that develop tolerance to ingested toxins (Sarnelle, 1993; Gragnani, Scheffer & Rinaldi, 1999; Gustafsson *et al.*, 2005; Sarnelle *et al.*, 2010). An improved efficiency for the physiological detoxification of ingested toxins would probably increase the potential for the zooplankton to control blooms. However, sufficient physiological tolerance in large generalist grazers is rare (Ghadouani *et al.*, 2004; Wilson *et al.*, 2006; Tillmanns *et al.*, 2008).

Despite the higher tolerance of generalists compared with selective grazers, most are not tolerant enough to ingest significant amounts of cyanobacteria (Tillmanns *et al.*, 2008). Although smaller cladocerans may develop stronger tolerance to ingested cyanobacteria compared with larger *Daphnia* (Guo & Xie, 2006; Davis & Gobler, 2011), large cyanobacterial colonies/filaments are typically too big to be ingested by such small grazers at a significant rate (Fulton & Paerl, 1987; Bouvy *et al.*, 2001; Ka *et al.*, 2012), reducing their potential to control blooms. Thus, while large grazer size, physiological tolerance and generalist grazing are all necessary traits for bloom control, these may be insufficient.

The timing of the bloom in relation to the abundance of large-bodied *Daphnia* may also be a critical factor determining potential for controlling cyanobacteria. There are only a handful of field observations showing that zooplankton can prevent cyanobacterial blooms in the absence of zooplanktivory (Sarnelle, 1993; Sarnelle *et al*., 2010). Among such examples, bloom control seems to be temporary and occurs if the tolerant zooplankton grazers reach high abundances before cyanobacteria begin to dominate the phytoplankton (Elser *et al*., 2000; Sarnelle, 2007). Thus, there may be a limited window of opportunity for generalist zooplankton grazers to prevent blooms before cyanobacteria get established.

The recent case of a *Daphnia pulicaria* clone grazing down an already established *Microcystis* bloom in an experimental fishless pond is a unique example in this context (Chislock *et al*., 2013). Although an exception, this case demonstrates that large-bodied generalist feeding *Daphnia* may indeed develop sufficient tolerance to overcome toxicity, grow and reproduce on a cyanobacterial diet and control an established bloom. While examples of tolerant *Daphnia* strains are rare, they may become more common in the future, either because of longer bloom exposure or as previously unrecognised strains are discovered.

As we begin to understand the molecular basis for the detoxification of cyanobacterial metabolites (Schwarzenberger *et al*., 2012; Mou *et al*., 2013), the option of modifying genetically large *Daphnia* species, so that they tolerate cyanobacteria in the diet, may be attempted in the near future. Transferring genes responsible for the detoxification of cyanobacterial metabolites into large *Daphnia* clones may one day produce generalist grazers with an improved efficiency for detoxifying cyanobacteria. Such tolerant clones could be in demand as a quick fix management tool for controlling blooms. However, the prospects for transgenic cyanotolerant *Daphnia* clones as a solution for long-term bloom control would still be low. From a practical point of view, the large diversity of inhibitory and toxic metabolites produced by cyanobacteria would make it unlikely that the effort would succeed. Assuming the practical issues can be resolved, using transgenic clones for the long-term control of blooms would still be problematic. While such tolerant zooplankton might control blooms at first, strong grazing pressure would select for the rapid evolution of cyanobacteria with increased toxicity and colony/filament size, eventually overcoming the tolerance traits of transgenic zooplankton.

Unless the physical and chemical causes of cyanobacterial dominance are diminished, tolerant zooplankton grazers are unlikely to control blooms in the long term. Although Chislock *et al.* (2013) showed that tolerant grazers could temporarily graze down cyanobacterial blooms and shift the system to a clear water state, this would only be maintained by a concurrent reduction in nutrient inputs (Mitra & Flynn, 2006). Finally, fish predation pressure is generally high in eutrophic lakes, suggesting that any large, efficient herbivore, transgenic or not, will eventually end up as fish food.

Zooplankton adaptations resulting in coexistence with blooms

Despite several recent examples of copepods and cladocerans ingesting cyanobacteria in natural systems (Sarnelle, 1993; Davis & Gobler, 2011; Ka *et al*., 2012), and although direct grazing effects may be important for bloom dynamics at certain times (Sarnelle & Wilson, 2005; Sarnelle, 2007), zooplankton tend to coexist with, rather than eliminate, cyanobacteria (Boon *et al*., 1994; Bouvy *et al*., 2001; Koski *et al*., 2002; Hu, Jorgensen & Zhang, 2006).

Selective feeding is a key adaptation that facilitates coexistence with blooms (Kirk & Gilbert, 1992; Kurmayer & Juttner, 1999). Typically, copepods are the most efficient in selective feeding among all the zooplankton as they can reject inedible food particles without inhibiting the ingestion of edible particles. However, some copepods can tolerate the ingestion of filamentous cyanobacteria (Engstrom-Ost *et al*., 2002; Panosso *et al*., 2003; Ka *et al*., 2012), and partial grazing by copepods may shorten the filament length of less toxic strains of cyanobacteria, such as *Cylindrospermopsis* and *Anabaena*, making them available to smaller cladocerans (Haney, 1987; Bouvy *et al*., 2001; Panosso *et al*., 2003; Chan *et al*., 2004). Nevertheless, more nutritious (non-cyanobacterial) food is usually preferred when available, reducing the grazing effect on blooms (DeMott, 1989).

Large-bodied *Daphnia* species are also known to coexist with cyanobacteria through a form of inefficient feeding selection that occurs when grazing is inhibited in the presence of certain cyanobacterial strains or cells with a particular morphology. However, this type of coexistence appears to be limited to cases where cyanobacterial blooms have a patchy distribution (Benndorf & Henning, 1989; Semyalo, Rohrlack & Larsson, 2009). Under this scenario, *Daphnia* continue grazing on edible phytoplankton by finding areas free from inhibitory cyanobacteria, causing a weak selection towards edible food. Yet, this mode does not provide a benefit during intense blooms, where patches of edible food may be reduced below food-limiting abundances. In such intense blooms, the ability to graze on edible food while avoiding toxic food stands out as the successful adaptation as it offers the most efficient solution to overcoming the ingestion of toxic food (DeMott & Moxter, 1991).

Smaller body size may be an advantage in generalist cladoceran grazers for preventing significant ingestion of large cyanobacterial colonies or filaments and resulting in coexistence with cyanobacteria (Haney, 1987; Hansson *et al.*, 2007; Davis & Gobler, 2011). Moreover, some small cladocerans, such as *Bosmina,* are dual-mode grazers, switching between raptorial and filter feeding (Cyr & Curtis, 1999), which may result in an intermediate feeding selectivity somewhere between generalist *Daphnia* and highly selective copepods.

Accordingly, waters experiencing more intense blooms, such as the tropical eutrophic reservoirs of South America, are dominated by copepods or smaller cladocerans that coexist with semipermanent blooms where >95% of the phytoplankton biomass consists of cyanobacteria for several months (Bouvy *et al.*, 2001; Souza *et al.*, 2008). Adaptations that promote coexistence of zooplankton by reducing the ingestion of toxic cyanobacteria (i.e. small size, selective grazing) also imply lower mortality rates of cyanobacteria due to grazing (Gragnani *et al.*, 1999; Rondel *et al.*, 2008). This weak link between zooplankton and cyanobacteria may be a self-stabilising process (Mitra & Flynn, 2006) that is likely to continue under future climate change scenarios (Hansson *et al.*, 2013).

How do cyanobacteria respond to zooplankton grazers?

While we are beginning to learn about how short-term exposure to cyanobacteria induces adaptive responses in zooplankton, only a handful of studies have looked into the induced or adaptive responses of cyanobacteria to increased grazing pressure. Both the presence and the grazing of zooplankton have been shown to increase toxin production (Jang *et al.*, 2003) and may increase colony size (Jarvis, Hart & Combrink, 1987). In turn, larger colonies are associated with higher concentrations of toxins (Kurmayer *et al.*, 2003). Increased grazing by generalist *Daphnia galeata* has been linked to the increase in microcystin-producing strains of *Microcystis* (Benndorf & Henning, 1989). Similarly, depending on the effectiveness of specific detection cues used by copepods, the degree of selective feeding on non-toxic strains may promote the abundance of toxic cyanobacteria genotypes, although this has been difficult to demonstrate due to the various factors that affect toxin production in nature (Gorokhova & Engstrom-Ost, 2009).

A major problem in this context is the lack of substantial evidence concerning the function of cyanobacterial toxins as grazer defences. Curiously, although widely accepted as grazing defences against zooplankton, the evolutionary roles of cyanobacterial secondary metabolites are essentially unknown. They have been shown to involve multiple properties, acting as grazing deterrents or cues (Kurmayer & Juttner, 1999), enzyme inhibitors (Rohrlack *et al.*, 2004; Von Elert *et al.*, 2005), toxins (Wiegand & Pflugmacher, 2005) and allelopathic compounds (Leflaive & Ten-Hage, 2007). Ultimately, these metabolites may have more than one ecological or physiological function, and zooplankton responses vary remarkably with species (Kurmayer & Juttner, 1999; Engstrom *et al.*, 2000; Ger *et al.*, 2010b). After all, no clear effect of the identified toxins has been shown across zooplankton species (Wilson *et al.*, 2006; Tillmanns *et al.*, 2008). New toxins are routinely identified (Von Elert *et al.*, 2005), and unidentified compounds with toxic or inhibitory effects are common (Lurling, 2003). As the production of toxins, such as microcystins, probably evolved long before animals appeared on the planet, such compounds might have arisen for other reasons than defence against zooplankton grazing (Rantala *et al.*, 2004).

Another key factor in understanding the function of cyanobacterial secondary metabolites is that the prokaryotic cyanobacteria evolve by different processes and at different rates than their eukaryote grazers. The production of cyanobacterial toxins is regulated by biosynthetic gene clusters, such as the microcystin synthetase (*mcy*). It is now evident that such gene clusters may be among life's fastest evolving genetic units, due to the relatively short replication time of their prokaryotic hosts and also to horizontal gene transfer (Fischbach, Walsh & Clardy, 2008; Ostermaier *et al.*, 2013). In fact, the latter may be the dominant driver of peptide evolution and diversity in prokaryotes, including cyanobacterial toxins (Treangen & Rocha, 2011). Thus, horizontal gene transfer stands out as a critical process for understanding the coevolutionary dynamics between zooplankton and cyanobacterial defences.

What are the plankton dynamics during prolonged blooms?

This is a major and stimulating question that is critical for understanding plankton ecology in a warmer and more eutrophic planet. Ultimately, the outcome of plankton dynamics experiencing longer blooms will depend, at least in part, on the specific adaptations of the tolerant zooplankton and their coupling with cyanobacteria. The extent of zooplankton grazing on cyanobacteria probably regulates several food-web processes, including the toxin production of cyanobacteria (Jang *et al.*, 2007; Gorokhova & Engstrom-Ost, 2009), competition between cyanobacteria and other phytoplankton (Wang *et al.*, 2010), bioaccumulation of toxins (Ibelings & Chorus, 2007; Miller *et al.*, 2010) and the flow of carbon from autochthonous primary producers through the food web (Pace, Cole & Carpenter, 1998; Kim, Hwang & Joo, 2000; Work & Havens, 2003; Davis *et al.*, 2012).

Copepods may be expected to facilitate cyanobacteria by grazing selectively on their phytoplankton competitors (Wang *et al.*, 2010), resulting in more persistent blooms (Scheffer & Rinaldi, 2000; Mitra & Flynn, 2006). Although significant, such positive species interactions that result in facilitation are often overlooked in ecology (Bruno, Stachowicz & Bertness, 2003). If grazing on cyanobacteria is intense, as it would be with tolerant and large cladocerans, zooplankton may accumulate cyanobacterial metabolites, potentially creating toxicity for their own predators (Kozlowsky-Suzuki, Wilson & Ferrao, 2012).

Ecosystem processes in eutrophic systems may largely depend on the fate of cyanobacterial carbon that accumulates during blooms (Dickman *et al.*, 2008; Brett *et al.*, 2009). The most significant grazers of dead or live cyanobacteria during blooms may be heterotrophic or mixotrophic protists (Van Wichelen *et al.*, 2010). In fact, there is evidence that several protist species, especially ciliates, not only ingest but specialise on and grow on a diet of colonial or filamentous cyanobacteria alone (Fyda, Fialkowska & Pajdak-Stos, 2010; Combes *et al.*, 2013). Results from these and other studies indicate that ciliates, phagotrophic flagellates and amoebae may also play important roles in the detoxification of microcystins (Bec, Martin-Creuzburg & Von Elert, 2006; Wilken *et al.*, 2010). Hence, increasing blooms can boost the abundance of heterotrophic protists that graze on cyanobacteria and thereby provide an abundant and potentially good quality food for zooplankton.

Recent work on the trophic upgrading of fatty acids in cyanobacterial cells by phagotrophic heterotrophic nanoflagellates (HNF) shows that cyanobacterial detritus may become a high-quality food source to zooplankton (Park *et al.*, 2003). In another study, the somatic growth rate of the zooplankton *Daphnia magna* fed HNF raised on toxic *Microcystis* was identical to those fed the conventional green algal good food *Scenedesmus*, although having an intermediate step still resulted in carbon loss (Bec *et al.*, 2006). Remarkably, the HNF *Paraphysomonas* increased the food quality of dead *Microcystis* cells in these studies. Grazing on heterotrophic microbes may explain how some copepods coexist and dominate zooplankton biomass during heavy cyanobacterial blooms (>99% of phytoplankton) in tropical systems (Bouvy *et al.*, 2001).

When edible phytoplankton is scarce, selectively feeding zooplankton can often shift grazing from autotrophic carbon to heterotrophic protists and bacteria (DeMott, 1989; Work & Havens, 2003). Both copepods and cladocerans are omnivores, grazing heavily on heterotrophic protists, resulting in trophic cascades between the larger crustacean grazers, the smaller microbial grazers (e.g. ciliates, flagellates) and phytoplankton (Pace *et al.*, 1998; Zollner *et al.*, 2003). Further, copepods are known to switch between heterotrophic and phytoplankton food chains depending on food availability (Stibor *et al.*, 2004). However, the accumulation of cyanobacteria biomass during blooms indicates that carbon fixed must flow through the microbial food web before passing to the zooplankton (Elser & Goldman, 1991; Ghadouani, Pinel-Alloul & Prepas, 2003; Davis *et al.*, 2012). Consequently, eutrophication is expected to result in reduced trophic transfer efficiency associated with the increased role of intermediary heterotrophic microbe grazers (Fig. 1).

Understanding cyanobacteria–zooplankton interactions in a more eutrophic world would be incomplete without some consideration of the expected proliferation of omnivorous fish that feed on both phyto- and zooplankton, such as the Nile Tilapia (*Oreochromis niloticus*) and various carp species. Such fish are common in tropical eutrophic waters and can tolerate and ingest significant amounts of toxic cyanobacteria (Xie & Liu, 2001; Rondel *et al.*, 2008). However, fish omnivory may inhibit cascades and reduce the potential for the top-down control of cyanobacteria (Attayde & Menezes, 2008). Moreover, omnivorous fish may shift the zooplankton community to smaller, more evasive (and specialist) species, such as copepods and rotifers, by grazing on the larger and generalist daphniids (Okun *et al.*, 2008). Thus, in addition to cyanobacterial defences, increased fish omnivory can also uncouple zooplankton from cyanobacteria.

Like fish, benthic filter feeders can also change the abundance of cyanobacteria; especially dreissenid mussels have been identified as ecosystem engineers (McLaughlan & Aldridge, 2013). Dreissenids generally lead to a decline in phytoplankton and zooplankton biomass, whereas macrophytes and littoral zoobenthos increase (Higgins & Vander Zanden, 2010). Experiments have shown that the mussels might graze down

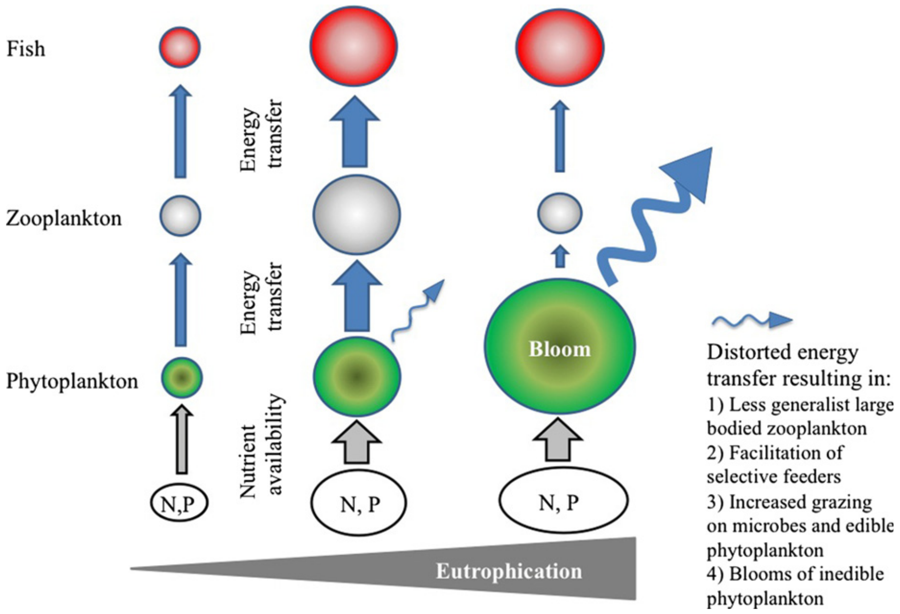


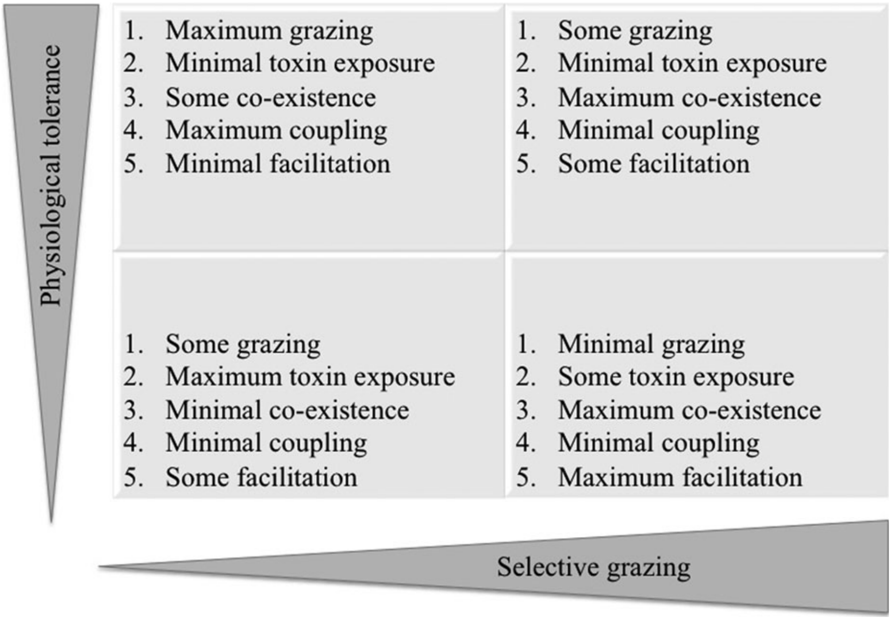
Fig. 1 A conceptual model showing the expected relationship of the trophic transfer of energy between primary producers and zooplankton, across a gradient of eutrophication. As eutrophication proceeds, the nutrient availability fuels phytoplankton biomass, which is efficiently transferred to zooplankton via high grazing and thus strong trophic coupling, with a relatively minor transfer of energy to the heterotrophic microbial food web. At higher levels of eutrophication where the phytoplankton is dominated by inedible or toxic cyanobacteria, the increased pool of primary production carbon is not directly grazed by zooplankton due to cyanobacterial attributes and defences (i.e. morphology, toxicity, nutrient deficiency, digestion resistance). Thus, most of the primary production energy and organic matter is diverted to heterotrophic microbes instead of zooplankton. The consequences of such blooms on plankton interactions include the facilitation of specialist feeders, increased zooplankton grazing on microbial food and, subsequently, a weaker zooplankton–phytoplankton coupling with potentially less energy or carbon available higher in the web. Selective zooplankton grazing on 'edible' phytoplankton may also facilitate cyanobacteria by eliminating competitors for primary production.

cyanobacteria with their relatively large filtering capacity (Dionisio Pires *et al*., 2005a; Kirsch & Dzialowski, 2012). However, filtration of *Dreissena* on *Microcystis* ceased above a colony size threshold (White & Sarnelle, 2014). Further, while dreissenids may exert a positive effect on cyanobacteria, this seems restricted to waters with low-to-moderate total phosphorus concentrations (Sarnelle *et al*., 2012). Thus, dreissenids may have the potential to control cyanobacteria in a more eutrophic world (Sarnelle *et al*., 2012) and may benefit from expected climate change (Gallardo & Aldridge, 2013). Several studies have concluded that the abundant mussel population of Lake IJsselmeer (the Netherlands) is controlling phytoplankton (e.g. Dionisio Pires *et al*., 2005b). However, in July 2006, during a heatwave (predicted to become more frequent in the near future), massive blooms occurred with phycocyanine concentrations of 200–250 mg m^{-3} covering also the south part of the lake (see http://www.kennislink.nl/upload/158556_276_1161096801164-blauwalg_beelden.jpg for ESA's ENVISAT images). Hence, it remains to be seen whether these mussels are indeed capable of controlling cyanobacteria in a changing world.

What approaches are necessary to understand the coevolutionary dynamics shaping cyanobacteria–zooplankton interactions?

Earlier studies have mostly overlooked that zooplankton and cyanobacteria have probably been coevolving for a very long time indeed. Increasing bloom duration and intensity can be expected to select for adaptive zooplankton traits, which determine what grazers eat when faced with cyanobacteria (outlined in Fig. 2). However, a number of questions must be resolved before predictions can be fully tested and can be summarised as the following:

1. What are the ecological outcomes of rapid evolutionary changes among cyanobacteria and zooplankton?
2. Can we expect tolerant zooplankton that may be able to control blooms, or should we be concerned with the effects of selective grazers in stabilising blooms?
3. What is the nature and fitness cost of induced (phenotypic) or genotypic zooplankton adaptations to increased exposure to cyanobacteria?
4. How do cyanobacteria adapt to zooplankton grazing pressure (e.g. morphology, toxin production)?



1. Maximum grazing 2. Minimal toxin exposure 3. Some co-existence 4. Maximum coupling 5. Minimal facilitation	1. Some grazing 2. Minimal toxin exposure 3. Maximum co-existence 4. Minimal coupling 5. Some facilitation
1. Some grazing 2. Maximum toxin exposure 3. Minimal co-existence 4. Minimal coupling 5. Some facilitation	1. Minimal grazing 2. Some toxin exposure 3. Maximum co-existence 4. Minimal coupling 5. Maximum facilitation

Fig. 2 Increased cyanobacteria blooms are likely to select for better adapted zooplankton, whose fitness-enhancing traits may regulate trophic coupling between phytoplankton and zooplankton, food-web complexity and the indirect facilitation of cyanobacteria. The type and relative degree of zooplankton adaptations can determine the possible outcomes of plankton dynamics, which include, respectively: (1) how much cyanobacteria is grazed, with implications on the potential for biomanipulation using zooplankton grazing (top-down control), (2) the extent of cyanobacterial toxin exposure causing reduced zooplankton fitness, (3) the potential for coexistence of cyanobacteria and zooplankton, (4) the relative magnitude of the cyanobacteria–zooplankton coupling and (5) the potential for the facilitation of cyanobacteria via selective grazing. Zooplankton are only expected to suffer reduced fitness when they lack efficient physiological tolerance to ingested cyanobacterial metabolites and when they are unselective grazers. Most possible cases thus result in a relatively uncoupled coexistence between the two groups, with different ecological implications, which are presented as hypotheses here for future studies. Trophic coupling would be inversely proportional to the degree of selective feeding and toxin exposure and positively proportional to the potential for long-term grazing on cyanobacteria.

5. Which of the cyanobacterial metabolites function as grazer deterrents?

6. How do heterotrophic protozoan grazers affect the abundance, toxicity and food quality of cyanobacteria?

7. Do tropical eutrophic systems with semipermanent blooms provide useful examples of the future of temperate waters in a more eutrophic world?

The theoretical aspects of plankton ecology have not incorporated recent observations regarding the flexibility in the adaptive traits of zooplankton for dealing with cyanobacterial defences (Wilson & Hay, 2007; Sarnelle *et al*., 2010; Ger *et al*., 2011), nor the implications of trophic upgrading of cyanobacterial cells by heterotrophic eukaryotic protists (Park *et al*., 2003; Bec *et al*., 2006). Both modelling and experimental studies should be updated to incorporate the genetic (i.e. natural selection of tolerant genotypes) and phenotypic (i.e. induced acclimation of individuals) flexibility in zooplankton responses to previous exposure to cyanobacteria. Recent sequencing of the entire genomes of the cladoceran *Daphnia pulex* and the copepod *Eurytemora affinis* opens up many opportunities for studying genetic and inducible mechanisms of physiological tolerance, and molecular tools can be very useful to understand the genetic basis of zooplankton tolerance to cyanobacterial toxins or inhibitors (Stillman *et al*., 2008; Schwarzenberger *et al*., 2012). For example, the molecular basis of improved tolerance in *Daphnia* to cyanobacterial protease inhibitors offers a preview of a formerly unknown array of fitness-enhancing traits in zooplankton (Schwarzenberger *et al*., 2012).

The nature of inducible cyanobacterial defences in response to grazer infochemicals also deserves more study (Jang *et al*., 2007). Zooplankton effects on cyanobacterial gene expression (via transcriptome sequencing) and the proliferation of toxic genotypes are essentially unknown. The relative effect of cyanobacterial morphology versus toxicity as a defence from zooplankton grazing also emerges as an important yet understudied topic. Finally, since strains of both toxic and non-toxic cyanobacteria can cause comparable damage to zooplankton fitness, the unsystematic designation of toxicity based on a single well-identified acute toxin (e.g. microcystin, saxitoxin) is flawed, and the role of less identified secondary metabolites must be considered (Tillmanns *et al.*, 2008). Solely focussing on zooplankton responses would ignore the fact that toxin production and morphology can be phytoplankton traits selected in response to more tolerant grazers (Selander *et al.*, 2006).

The cumulative evidence considered here suggests that the outcome of zooplankton–cyanobacteria interactions is regulated by adaptive responses between grazer and grazed, at the individual, micro- and macroevolutionary scales. The short generation time of planktonic organisms means that we may be witnessing the ecological and evolutionary consequences of eutrophication simultaneously. Distinguishing among these mechanisms is possible and will be a critical yet challenging step for understanding bloom-dominated ecosystems (Dam, 2013). This will require a move towards the standardisation of experiments with respect to the physiological state as well as the genetic background of the organisms being studied (both zooplankton and cyanobacteria).

In summary, increased exposure to cyanobacteria is expected to shift the zooplankton community to more adapted species, to select for better adapted genotypes within those species and to induce physiological or behavioural traits within the lifetime of individual zooplankton. Moreover, the accumulation of cyanobacterial biomass represents an increasing source of energy to the heterotrophic microbial prey of zooplankton (Bec *et al.*, 2006; Davis *et al.*, 2012), reducing trophic transfer efficiency (Brett *et al.*, 2009) and indicating a minimal potential for the control of blooms by zooplankton (Pace *et al.*, 1999). However, the mechanism behind such changes, as well as their potential effects on plankton dynamics (i.e. bloom stability and toxicity), is largely unknown. Thus, understanding the response of planktonic systems to increasing blooms will require a closer look into the interaction between the concurrent ecological and microevolutionary processes that govern cyanobacteria–zooplankton interactions.

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