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Review

The interaction between cyanobacteria and zooplankton in a more eutrophic world

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ABSTRACT

As blooms of cyanobacteria expand and intensify in freshwater systems globally, there is increasing interest in their ecological effects. In addition to being public health hazards, cyanobacteria have long been considered a poor quality food for key zooplankton grazers that link phytoplankton to higher trophic levels. While past laboratory studies have found negative effects of nutritional constraints and defensive traits (i.e., toxicity and colonial or filamentous morphology) on the fitness of large generalist grazers (i.e., *Daphnia*), cyanobacterial blooms often co-exist with high biomass of small-bodied zooplankton in nature. Indeed, recent studies highlight the remarkable diversity and flexibility in zooplankton responses to cyanobacterial prey. Reviewed here are results from a wide range of laboratory and field experiments examining the interaction of cyanobacteria and a diverse zooplankton taxa including cladocerans, copepods, and heterotrophic protists from temperate to tropical freshwater systems. This synthesis shows that longer exposure to cyanobacteria can shift zooplankton communities toward better-adapted species, select for more tolerant genotypes within a species, and induce traits within the lifetime of individual zooplankton. In turn, the function of bloom-dominated plankton ecosystems, the coupling between primary producers and grazers, the stability of blooms, and the potential to use top down biomanipulation for controlling cyanobacteria depend largely on the species, abundance, and traits of interacting cyanobacteria and zooplankton. Understanding the drivers and consequences of zooplankton traits, such as physiological detoxification and selective vs. generalist grazing behavior, are therefore of major importance for future studies. Ultimately, co-evolutionary dynamics between cyanobacteria and their grazers may emerge as a critical regulator of blooms.

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1. Introduction

The ongoing and predicted global increase in cyanobacterial dominance is one of the most visible threats to the ecology of lakes, rivers, and some estuaries (Paerl and Huisman, 2008). The structure and function of aquatic ecosystems largely depends on the quality and quantity of primary production for zooplankton grazers. While high quality phytoplankton enable efficient transfer of carbon and energy to higher trophic levels, cyanobacterial traits (e.g., toxicity, size, nutrition) may reduce zooplankton fitness (Wilson et al., 2006) and the ecological coupling between primary producers and their grazers (Elser and Goldman, 1991). Indeed, this trophic uncoupling intensifies under highly eutrophic conditions when cyanobacteria dominate phytoplankton communities (Auer et al., 2004). Yet, zooplankton often co-exist with toxic cyanobacterial blooms and the function of plankton ecosystems depends also on the traits and abundance of zooplankton. For example, while copepods may facilitate cyanobacteria (Hong et al., 2013), high abundances of generalist grazers (i.e., *Daphnia*) may control blooms when released from planktivorous fish predation (Sarnelle, 2007). Hence, although bloom-forming cyanobacteria have historically been considered a poor quality food with weak links to zooplankton, examples of strong top down bloom control emphasize the complexity of cyanobacteria–zooplankton interactions.

The attributes that make cyanobacteria a low quality food are well-studied (Porter, 1977; Porter and Orcutt, 1980). Toxicity and morphology are considered key traits limiting the edibility of cyanobacteria by zooplankton. Early studies suggested that unidentified toxic compounds produced by cyanobacteria caused mortality in key zooplankton grazers, such as *Daphnia* (Lampert, 1981). The large colonial or filamentous morphologies of some cyanobacterial genera have also been shown to disrupt grazing in zooplankton (Webster and Porter, 1978; Lynch, 1980; Fulton and Paerl, 1987). Over time, these traits have been viewed as putative anti-grazer defenses in phytoplankton (Pohnert et al., 2007). Moreover, cyanobacteria have been shown to lack essential lipids, thus being nutritionally inadequate for most zooplankton, including cladocerans and copepods, and further reducing the trophic transfer efficiency (Müller-Navarra et al., 2000; Dickman et al., 2008).

Despite decades of research, cyanobacteria-zooplankton interactions and downstream effects on trophic dynamics remain elusive. Historically, the focus has been on studying the grazing defenses of cyanobacteria and their effects of zooplankton. Several cyanobacterial secondary metabolites, such as microcystins (MCs), were shown to have negative physiological effects on zooplankton (Rohrlack et al., 1999; Lürling and Van Der Grinten, 2003). Yet, soon it became clear that negative effects on zooplankton were not necessarily due to well-studied toxins (Wilson et al., 2006), highlighting the unknown diversity of cyanobacterial metabolites (Sadler and Von Elert, 2014a,b). Moreover, several studies have confirmed that zooplankton tolerance is highly variable among and within species via the rapid evolution of local adaptation (Hairston et al., 1999; Tillmanns et al., 2008; Kuster and Von Elert, 2013).

Given the greater awareness of freshwater harmful algal blooms in the 1980s, studies on the use of biomanipulation (i.e., facilitation of large-bodied zooplankton grazers via removal of planktivorous fishes) to control the abundance of nuisance cyanobacteria increased (Vanni, 1984; Sarnelle, 1992). In temperate lakes with relatively short bloom durations, fish removal boosts large-bodied cladocerans, such as *Daphnia*, leading to strong suppression of phytoplankton and cyanobacteria (Shapiro et al., 1975; Meijer et al., 1994). Thus, despite the anti-grazer defenses mentioned above, top-down control of established toxic cyanobacteria blooms in temperate waters may be possible (Chislock et al., 2013a,b; Ekvall et al., 2014). The results depend on the abundance and tolerance traits of local *Daphnia* populations and if the prevailing cyanobacterial community is within the edible size range. Yet, in warmer climates with longer bloom durations, *Daphnia* are rare, smaller zooplankton dominate, and there is more omnivory resulting in a weaker trophic cascade (Jeppesen et al., 2005). Several experiments in warmer climates have described the trophic cascade uncoupling at the phytoplankton-zooplankton link (Hunt and Matveev, 2005; Lacerot et al., 2013), especially in more eutrophic waters where cyanobacteria dominate primary production (Rondel et al., 2008). These studies support the variance-inedibility hypothesis (Holt and Loreau, 2002), which states that trophic cascades only occur when trophic levels are dominated by species edible to the next trophic level (Polis et al., 2000). Hence, the transfer of energy and carbon during blooms depends on the "edibility" of cyanobacteria, which is ultimately shaped by the traits of both zooplankton (e.g., tolerance) and cyanobacteria (e.g., size, toxicity).

Plankton traits however, are not fixed, and as blooms increase interaction strength between zooplankton and cyanobacteria, their traits can evolve rapidly (Lemaire et al., 2011). Increased cyanobacteria can induce phenotypic adaptations over the lifetime of individual zooplankton (Gustafsson et al., 2005), and select for better-adapted zooplankton genotypes (Hairston et al., 1999) or species (Hansson et al., 2007a,b). Thus, although cyanobacteria have traits that negatively affect zooplankton, insight into the variable nature of interactions between grazers and their prey is only beginning. Accordingly, the research fields necessary for understanding plankton ecology in eutrophic, cyanobacteria-dominated freshwaters are updated and synthesized here. These include the physiology, mechanistic underpinning, and variability in cyanobacterial and zooplankton traits (Section 2); the structure and function of cyanobacteria-dominated inland waters (Section 3); the emerging role of micro-evolutionary dynamics in plankton (Section 4); and eco-evolutionary implications of increased eutrophication on plankton dynamics (Section 5).

2. Physiological interactions between cyanobacteria and zooplankton

2.1. Traits of cyanobacteria affecting grazers

Cyanobacterial blooms occur when their growth exceeds losses from grazing and sedimentation. Given sufficient resources, blooms can only develop when cyanobacteria are not being heavily grazed. Although weak grazer pressure due to zooplanktivorous fish can trigger blooms, the uncoupling between cyanobacteria and zooplankton may persist without zooplanktivory (Elser and Goldman, 1991; Dickman et al., 2008; Rondel et al., 2008). Thus, the persistence of cyanobacteria blooms inherently indicates strong grazing resistance. In general, nutritional inadequacy, poor manageability and toxicity are viewed as the most crucial factors constraining the energy transfer from cyanobacteria to higher trophic levels (Porter and Orcutt, 1980).

2.1.1. Grazing defenses

Grazing and sedimentation are the major phytoplankton loss processes in freshwater systems (Reynolds, 1984). Yet, buoyancy control in cyanobacteria reduces sinking loss, leaving grazing as a major selection pressure for traits that reduce mortality. A straightforward strategy to withstand grazing losses is to grow to sizes that slow or prohibit zooplankton ingestion (Lehman, 1988). The typical colonial or filamentous morphology of many cyanobacterial taxa reduces zooplankton feeding rates in zooplankton (Fulton and Paerl, 1987, 1988) via mechanical interference when above critical concentrations (Gliwicz, 1990a,b). Low grazing rates on cyanobacteria however, are not only due to their morphology (Fulton and Paerl, 1988; Epp, 1996) and other traits such as "bad taste" or toxicity may be involved (DeMott and Moxter, 1991).

Cyanobacterial metabolites can reduce zooplankton fitness in laboratory studies (DeMott et al., 1991; Gilbert, 1990; Rohrlack et al., 1999, 2005; Wilson and Hay, 2007). These include the hepatotoxic microcystins (MCs) and nodularins, neurotoxic saxitoxins, alkaloids like cylindrospermopsin, and also protease inhibitors (e.g., microviridin, cyanopeptolins), though a large number of toxins probably remain unidentified (Sadler and Von Elert, 2014a,b). Overall, the multitude of cellular metabolites produced by a cyanobacterial strain and nutritional differences in experimental prey types (typically includes cyanobacteria and eukaryotic chlorophytes) has generally limited efforts in isolating the effects of individual metabolites from the ensemble of others (but see Wilson and Hay, 2007). For example, some zooplankton might use MCs or a related cue to avoid ingesting MC producing cells (Ger et al., 2011) and grazing was rapidly reduced in sensitive *Daphnia* exposed to extra-cellular products from cyanobacteria (Ostrofsky et al., 1983; Forsyth et al., 1992; Haney et al., 1995). Yet, the inhibitory effect of *Microcystis aeruginosa* on *Daphnia* feeding (Haney et al., 1994) was independent of MCs (Rohrlack et al., 1999; Kaebernick et al., 2001; Lürling and Van Der Grinten, 2003) and "mouse-killing" factors (Nizan et al., 1986).

Cyanobacterial metabolites, primarily those that are harmful to mammals, such as MCs, are presumed also toxic to zooplankton (Lampert, 1981). This has led to the hypothesis that cyanotoxins have evolved as defenses against zooplankton (Lampert, 1981; DeMott and Moxter, 1991). Yet, the genes for MC production appeared long before animals appeared on the planet, so the original evolutionary pressure selecting for these genes was not related to defense against metazoan grazers (Rantala et al., 2004). Nonetheless, when MCs enter tissues and cells they may be highly toxic to zooplankton through inhibition of phosphatases (DeMott and Dhawale, 1995). Toxicity is confirmed by experiments using purified dissolved MC-LR, which caused mortality in zooplankton species (DeMott et al., 1991; Ger et al., 2009). Yet, a meta-analysis yielded no influence of MC toxicity on zooplankton population growth rate and only marginal evidence of a MC toxicity influence on zooplankton survival overall, which was largely influenced by the repeated use of a single, toxic *Microcystis aeruginosa* strain (Wilson et al., 2006). Another meta-analysis revealed that while *Microcystis* had the largest negative effect on zooplankton population growth, the MC content had no effect on cladoceran or rotifer responses (Tillmanns et al., 2008). The poor correlation between cyanobacterial strains that produce varying amounts of well-studied toxins, such as MCs, and zooplankton growth or survival may be explained by the presence of unknown cyanobacterial secondary metabolites (Reinikainen et al., 2002a; Lürling and Van Der Grinten, 2003; Rohrlack et al., 2003; Ghadouani et al., 2004). *Microcystis* might produce numerous nonribosomal peptides other than MCs that may target major digestive proteases in *Daphnia*, cause mortality during molting or acute toxicity (e.g. Rohrlack et al., 2004; Von Elert et al., 2005; Blom et al., 2006). Given that cyanobacteria produce far more bioactive compounds than the selected few commonly studied (Sivonen and Börner, 2008), it seems advisable to take into account the whole suite of secondary metabolites and their synergistic effects when considering toxicity of cyanobacteria to zooplankton (Sadler and Von Elert, 2014a,b).

2.1.2. Nutritional quality of cyanobacteria

Cyanobacteria are widely acknowledged to be of poor nutritional quality for zooplankton (Gulati and DeMott, 1997; Müller-Navarra et al., 2000). Most zooplankton species grow slower, reproduce less, and generally have higher mortality when fed cyanobacteria alone compared to other more nutritionally replete phytoplankton taxa (i.e., cryptophytes and green algae) (Tillmanns et al., 2008). These nutritional effects primarily result from mismatches between the lipid content of cyanobacteria and their metazoan consumers (Von Elert et al., 2003). In particular, cyanobacteria generally lack essential fatty acids (e.g., polyunsaturated fatty acids, PUFAs) and sterols that are required for zooplankton growth and reproduction. Sterols place strong constraints on *Daphnia* growth and PUFAs may strongly affect reproduction of zooplankton consumers (Martin-Creuzburg et al., 2008; Martin-Creuzburg and von Elert, 2009). Evidence for these constraints has been provided by the use of lipid supplementation experiments, where different fatty acids (FA) were provided to the zooplankton consumer without otherwise altering their cyanobacterial food source (Von Elert, 2002; Ravet et al., 2003). Lipid supplementation increases the growth, reproduction, and survival of *Daphnia* consuming different cyanobacteria, but such effects vary with the type of supplementation (Von Elert, 2002). Measurements of the lipid content of cyanobacteria collected during blooms periods have shown low content of certain FAs, resulting in slower growth and less reproduction when fed to *Daphnia* (Müller-Navarra et al., 2000). While lipid constraints on zooplankton growth may be common, they may be transitory as in situ lipid supplementation may occur during bloom decay or from the ingestion of bacteria, protozoans and co-occurring phytoplankton in nature (Klein Breteler et al., 1999; Luo et al., 2015).

Negative effects on zooplankton grazers due to low lipid content may be further intensified by filamentous or large colonial cyanobacteria due to the mechanical inference during feeding as explained in Section 2.1.1. This leads to a high rejection rate of food particles and less intake per unit effort (Bednarska et al., 2014). Once ingested, mucilage sheaths or colonies may be highly resistant to digestion (Reynolds, 2007), which lowers the net assimilation efficiency of cyanobacteria. Some cyanobacteria may also release protease inhibitors while in the zooplankton digestive tract (Agrawal et al., 2005; Schwarzenberger et al., 2010) and thereby further reduce rates of digestion. These limits to digestion and assimilation would presumably reduce the net acquisition of all nutritional components (e.g., energy, N, P, and lipids) and exacerbate already low supplies of essential dietary lipids.

Given the effects of acute limitation of particular FAs and the toxicity from exposure to secondary metabolites, patterns of gene expression and downstream metabolic pathways in zooplankton are likely to be altered by ingestion of cyanobacteria. For example, consumption of *Microcystis* altered the expression of selected genes in *Daphnia* (Schwarzenberger et al., 2009). These changes in gene expression may be involved in responses reducing metabolic rates or may be specific to the particular form of limitation or damage created by exposure to the cyanobacteria. *Daphnia* feeding on the non-toxic cyanobacterium *Synechoccocus* increased their body alkaline phosphatase activity and P-content likely to increase the extraction and use efficiency of the limiting FA (Wagner and Frost, 2012). Such effects extend to the lipid profile of *Daphnia* bodies as well (Von Elert, 2002; Brett et al., 2006; Wacker and Martin-Creuzburg, 2007), and suggest that *Daphnia* may be able to reduce their requirements for particular FAs during their lifetime.

Less is known about the elemental composition of freshwater cyanobacteria. Variability in the C:N, C:P, and N:P ratios of cyanobacteria grown in culture has been found for several taxa (Geider and La Roche, 2002; Bertilsson et al., 2003). This elemental flexibility is a hallmark of primary producers, which elevate C:N and C:P ratios when experiencing acute nutrient-limitation under high light and C-availability (Sterner et al., 1997; Frost and Elser, 2002; Frost et al., 2005). Cyanobacteria have high N:P demands, which may place them at a competitively disadvantage to other phytoplankton under low N-supply (Hillebrand et al., 2013), and is intriguing given the long-standing paradigm that cyanobacterial blooms are promoted by low N:P ratios in lakes (Schindler, 1977). One potential explanation is that optimal N:P ratios vary among cyanobacterial taxa that fix N and those that do not (Elser, 1999). Variability in the elemental composition of cyanobacteria could have strong effects on zooplankton consumers, but this remains largely unstudied. Changes in C:N:P composition of cyanobacteria could amplify the physiological stress of low lipid content and yield an especially poor food quality for zooplankton (Wagner and Frost, 2012).

2.1.3. Phenotypic response of cyanobacteria to grazers (induced defenses)

Since grazing pressure in the pelagic varies both on temporal and spatial scales, the evolution of temporary defenses should be favored compared to constitutive (genetically fixed) defenses in phytoplankton (Clark and Harvell, 1992). Such inducible defenses can be an important adaptive strategy to reduce grazing losses and minimizing costs associated with the defense (Tollrian and Harvell, 1999). Major phytoplankton defensive strategies include adaptations in morphology, biochemical make-up (toxicity), life-history changes, and altered behavior (Van Donk et al., 2011), though relatively few studies address cyanobacteria, and the evidence for grazer-induced defenses in cyanobacteria is not overwhelming. Combining exposure experiments with recent advances in transcriptome sequencing may reveal the more complete metabolic response of cyanobacteria to grazers. Reviewed below is the available information on induced cyanobacteria defenses.

2.1.3.1. Morphology. Cyanobacteria may show striking morphological differences, between species, but also within the same strain (i.e., phenotypic plasticity). One of the most well known phenotypic alterations is the switch in *Microcystis* from its typical colonial appearance in the field to a unicellular form under laboratory conditions (Geng et al., 2013). Since two conflicting selection pressures exist – competition favoring small organisms that have the most efficient acquisition of resources (Reynolds, 1984) and predation favoring large grazer-resistant sizes (Lehman, 1988), the observed morphological differences in *Microcystis* may suggest an inducible defense. This is further supported by observations that colonial *Microcystis* suffer less grazing loss than unicellular morphotypes when exposed to generalist filter feeders, such as large-bodied cladocerans (Fulton and Paerl, 1988).

Results for zooplankton induced colony formation or filament aggregates in cyanobacteria are not conclusive. Filamentous cyanobacteria (*Aphanizomenon*) were observed as large grass-blade flakes in the presence of *Daphnia*, but dissociated within 48 h into single or small groups of filaments in their absence (Lynch, 1980). Zooplankton have caused minor increases in the number of *Microcystis* cells per colony (Jang et al., 2003; Ha et al., 2004) and aggregate formation only in a non-MC producing strain (Becker, 2010). Exposure to chemicals associated with *Daphnia* grazing caused colony formation in one out of eight strains (Van Gremberghe et al., 2009a), while exposure to direct *Daphnia* grazing generated large colonies in one out of four strains (Van Gremberghe et al., 2009b). In contrast, many studies failed to detect metazoan zooplankton induced colony or filamentous flake formation in cyanobacteria; neither induced by chemicals released from *Daphnia* (Fulton and Paerl, 1987) nor by live *Daphnia* (Yang et al., 2006). Similarly, the cyanobacterium *Nodularia spumigena* showed no morphological response when exposed directly or indirectly to its natural enemy, the copepod *Arcatia* cf. *bifilosa* (Lundgren et al., 2012). While less is known about the effect of protozoan grazers, studies show that they can induce relatively large *Microcystis* colonies (Burkert et al., 2001; Yang and Kong, 2012). Interestingly, colony formation in *Microcystis* was induced by the mixotrophic protozoan grazer *Ochromonas* but not by a copepod, cladoceran and rotifer grazer, which may be due to the toxin resistance of the protozoan and the sensitivity of the latter grazers (Yang et al., 2006). Field data are in favor of the hypothesis that unicells and small-sized colonies are protected from grazing when toxicity is strong (Benndorf and Henning, 1989).

2.1.3.2. Toxicity. If cyanotoxins, such as MCs, function as defense against grazers (Lampert, 1981; DeMott and Moxter, 1991), they could make suitable candidates when considering the induced defense hypothesis. A significant correlation between *Microcystis* MC content and grazer (*Daphnia*) biomass (Izydorczyk et al., 2008) supports this hypothesis, which is corroborated by laboratory studies reporting enhanced MC production in *Microcystis* exposed to zooplankton (Jang et al., 2003, 2007). Yet, others did not find such a MC response in *Microcystis* to *Daphnia* (Van Gremberghe et al., 2009b; Becker, 2010) or to the mixotrophic protozoan, *Ochromonas* (Wilken et al., 2010). Likewise, exposure (directly and indirectly) of the cyanobacterium, *Nodularia spumigena*, to the copepod grazer, *Arcatia* cf. *bifilosa*, did not lead to increased cell contents of the cyanotoxin, nodularin (Lundgren et al., 2012). In fact, some studies found the opposite: lower toxin levels in *N. spumigena* exposed to copepods when compared with those in the treatments without the grazers (Gorokhova and Engstrom-Ost, 2009). Interestingly, Pineda-Mendoza et al. (2014) found that infochemicals from *Daphnia* can either decrease or increase the production of MCs, depending on the bacterial community present.

Recently, Sadler and Von Elert (2014a,b) focused on two distinct classes of cyanobacterial peptides; the cyanopeptolins and the cyclamides, of which the former are known to act as protease inhibitors in zooplankton and the latter found to be toxic to fairy shrimps. These authors found an increase in the intracellular concentrations of those peptides caused by the presence of actively grazing *Daphnia* and proposed a role of these compounds as anti-herbivore defense in cyanobacteria. Although additional experiments are required to test this hypothesis, it is clear that the wide spectrum of cyanobacterial metabolites with putative defensive attributes against grazers goes well beyond MCs.

Overall, studies on zooplankton induced toxin production by cyanobacteria are limited. No studies have focused on other known cyanotoxins than the peptides presented here. A major challenge is to isolate the putative infochemical from other compounds that grazers excrete, including ammonia, which may also increase the toxin quota of *Microcystis* (Horst et al., 2014). Nevertheless, waterborne cues from calanoid copepods promoted increased production of paralytic shellfish poisons in the dinoflagellate *Alexandrium minutum* (Selander et al., 2006), which was a response specific to a single copepod grazer (Bergkvist et al., 2008). Such evidence supports that infochemicals – not nutrients excreted by zooplankton – may induce toxin production, at least in marine phytoplankton. Distinguishing the effects between selective grazing from grazer infochemicals or excretions is critical for future work on zooplankton induced cyanobacterial defenses.

2.1.3.3. Behavior/life-history. Reports on behavioral responses in cyanobacteria to grazers are very rare. The filamentous, mat-forming cyanobacterium, *Phormidium*, produces empty sheath endings under grazing pressure that allows active withdrawal of the trichomes inside the sheaths and provides protection against ciliate grazers (Fialkowska and Pajdak-stós, 1997). Notably, induced behavioral responses of phytoplankton responding to zooplankton grazers are well known (Selander et al., 2011; Latta et al., 2009). While these examples suggest a potential role, induced behavioral responses of cyanobacteria to grazers remains largely unexplored.

2.2. Zooplankton tolerance traits

Zooplankton are the primary link between phytoplankton and higher trophic levels. When the phytoplankton community is dominated by toxic, nutritionally poor, or inedible cyanobacteria, the coupling between phytoplankton and zooplankton weakens significantly (Elser and Goldman, 1991; Dickman et al., 2008; Rondel et al., 2008). Yet, zooplankton often co-exist with cyanobacterial blooms and have various adaptations to behaviorally avoid ingesting toxic doses and metabolize ingested toxins. Essentially, their response to cyanobacteria depend on two factors: (A) the amount of toxin-containing cells that are ingested, i.e., grazing behavior (Kirk and Gilbert, 1992), and (B) the assimilation and detoxification of ingested cyanobacterial metabolites (Pflugmacher et al., 1998). Over macro-evolutionary scales, zooplankton species more exposed to ingestion and assimilation of toxic cells are also more tolerant (DeMott et al., 1991). In addition to interspecific differences, there is also a large variability of tolerance within species (Wilson et al., 2006; Tillmanns et al., 2008). Tolerance can be induced (phenotypic plasticity, Gustafsson and Hansson, 2004), passed from mother to offspring (maternal effects, Gustafsson et al., 2005), or a heritable genotype trait (Hairston et al., 2001). Although phenotypic and genotypic variabilities have made it difficult to generalize about plankton ecology, research into the effects of previous cyanobacteria exposure on zooplankton tolerance is revealing the adaptive mechanisms that regulate toxin exposure and assimilation.

2.2.1. Grazing adaptations

The major route of cyanobacterial metabolite exposure for zooplankton to these metabolites is via the ingestion of cyanobacterial cells. Overall, mass specific ingestion rates are inversely proportional to zooplankton size, and smaller organisms ingest at higher rates compared to larger organisms (Sterner, 1989). Despite the negative relationship between size and mass-specific ingestion, *per capita* ingestion is proportional to body size. As the largest of the planktonic cladocerans, daphnids have the highest per individual grazing rates of all freshwater zooplankton (Hall et al., 1976). Freshwater cladocerans also have higher mass-specific filtration rates than copepods (Peters and Downing, 1984).

While differences in individual grazing rates are critical, prey selection is the key trait for tolerating cyanobacterial blooms for many zooplankton. Grazing selection is the ability to graze on nutritious prey while avoiding ingestion of harmful or inert particles. Copepods and rotifers are highly selective (DeMott, 1986) and can actively detect and avoid ingesting cyanobacteria from mixed prey (DeMott and Moxter, 1991). Indeed, copepods often co-exist with cyanobacterial dominance by uninhibited grazing on alternative prey (Bouvy et al., 2001; Koski et al., 2002).

Upon encountering cyanobacteria, copepods use multiple chemosensory signals including prey size, toxins, lipopolysaccharides, and unidentified lipophylic compounds as detection cues to avoid ingestion (Kurmayer and Jüttner, 1999; Engström et al., 2000; Ger et al., 2011). Yet, selectivity varies among species and significant ingestion of cyanobacteria can still occur (Panosso et al., 2003; Chan et al., 2004). Some copepods select against strains of cyanobacteria producing a known toxin, while others graze equally on cyanobacterial strains with contrasting toxin production (DeMott and Moxter, 1991; Ger et al., 2010b, 2011; Engström et al., 2000). Moreover, not all chemical detection cues are toxins, which can cause copepods to ingest toxic doses of cyanobacteria despite selective grazing (Ger et al., 2010a,b; Hong et al., 2013). Notably, the copepod *Eudiaptomus gracilis* improved its efficiency in the selective avoidance of *Microcystis* following a 5-day exposure, indicating that induced responses to cyanobacteria exposure may be common in other selective grazers (Ger et al., 2011).

In contrast, cladocerans are generalist grazers, with little ability to handle individual food particles (Kirk and Gilbert, 1992). While generalist grazing at high rates is advantageous when phytoplankton are nutritious, the cost during cyanobacterial blooms is reduced grazing on better quality food. The only option for cladocerans when faced with toxic cyanobacteria is to reject all food particles collected by the feeding apparatus (DeMott, 1986, 1989). Thus, *Daphnia* can hardly avoid ingesting toxic cyanobacteria, other than by reducing overall feeding rate (Ghadouani et al., 2004; Rohrlack et al., 2001). Although this serves as a useful trait when blooms are patchy (Benndorf and Henning, 1989), the fitness of *Daphnia* during long-term increased cyanobacterial dominance is reduced because of lower energy intake or ingestion of toxic cells (Lürling and Van Der Grinten, 2003; Ghadouani et al., 2004).

Importantly, some smaller cladocerans such as *Bosmina* can switch between filter and raptorial feeding, providing an intermediate degree of grazing selectivity between copepods and *Daphnia* (Cyr and Curtis, 1999).

Heterotrophic protozoans (microzooplankton) such as ciliates, naked amoebae, and flagellates ingest food particles via phagocytosis and may be important grazers on eukaryotic algae and cyanobacteria (Dryden and Wright, 1987; Sommer et al., 2012). Some ciliates and amoebae can engulf prey items several times their own length by breaking down trichomes or encapsulating individual cells from cyanobacterial colonies (Dryden and Wright, 1987). In addition, many naked amoebae are able to feed on distinct cyanobacterial morphotypes and have often been associated with mass proliferations of cyanobacteria (Van Wichelen et al., 2010). Hence, despite conventional assumptions, cyanobacterial toxicity, size or morphological defenses do not necessarily prevent grazing by protozoan microzooplankton (Dryden and Wright, 1987; Van Wichelen et al., 2012). Still, some protozoans display highly adaptive strategies in response to toxic cyanobacteria, including avoidance by selective digestion of cells and feeding selection of prey through chemotaxis (Urrutia-Cordero et al., 2013).

2.2.2. *Assimilation of toxins and physiological detoxification*

Upon ingestion of cyanobacterial cells, toxins are absorbed in zooplankton guts along with nutrients (Rohrlack et al., 1999). Ingested toxins appear to be metabolized via anti-oxidant enzymes including glutathione S-transferases (sGST) and catalase, which limit the assimilation of toxins (Pflugmacher et al., 1998), or are removed via transport mechanisms (Sadler and Von Elert, 2014a,b). Given practical difficulties to test the effect of ingested purified toxins directly, the standard method for comparing the detoxification efficiency of zooplankton is an acute toxicity test with the suspect cyanobacterial metabolite provided in the dissolved form. Multiple studies have confirmed that the efficiency of detoxification to microcystin (MC-LR) varies significantly among different zooplankton species. Interestingly, the most tolerant zooplankton identified to date is a ciliate ($LC_{50} = 252\ \mathrm{mg\ L^{-1}}$ MC-LR), while cladocerans are an order of magnitude more sensitive (LC_{50} between 21.4 and $9.6\ \mathrm{mg\ L^{-1}}$ MC-LR), and copepods appear as the least tolerant (as low as $0.27\ \mathrm{mg\ L^{-1}}$ MC-LR) (see references in Ger et al., 2009). In addition to standard acute toxicity assays, it is now also possible to study the physiology of zooplankton tolerance to cyanobacterial toxins via the activity of detoxification enzymes and their gene expression (Schwarzenberger et al., 2012).

A field study comparing MC levels in *Daphnia* tissue from two lakes having contrasting levels of toxic cyanobacteria found higher levels of detoxification enzymes and lower levels of MC accumulated in *Daphnia* tissues from the cyanobacteria dominated lake (Wojtal-Frankiewicz et al., 2013). This suggests stronger detoxification in *Daphnia* populations with longer exposure history to cyanobacteria, supporting the hypothesis that improved tolerance among zooplankton populations is due to more efficient physiological detoxification.

Assimilation avoidance of ingested toxins may be another key regulator of tolerance among *Daphnia* genotypes. MCs appear to be readily assimilated by "sensitive" *Daphnia* (i.e., genotypes that are strongly inhibited by toxic *Microcystis*), either due to ingestion of toxic cells or the uptake of dissolved MCs from water (Ferrao-Filho et al., 2014; Rohrlack et al., 2005). In contrast, "tolerant" *Daphnia* genotypes (i.e., able to survive and reproduce in the presence of high concentrations of toxic cyanobacteria – see Chislock et al., 2013b) may be better at avoiding the assimilation of MCs from the gut or surrounding medium. Tolerant *Daphnia* grazing on MC or cyanopeptolin containing cells have been shown to shift these metabolites from the particle (cellular) to the dissolved fraction with little change in their total concentration (Sadler and Von Elert, 2014a,b), suggesting no assimilation, and in this case no detoxification. In addition, a comparison of gene expression in tolerant *Daphnia* feeding on a MC-producing *Microcystis* genotype (PCC7906) vs. an identical genotype with the MC gene "knocked out" (PCC7806MUT) showed differential expression of "transporter" genes that may be involved in assimilation (Schwarzenberger et al., 2014). Transporter genes were down regulated in animals feeding on MC-containing cells, also suggesting assimilation avoidance (Schwarzenberger et al., 2014).

Fewer studies have focused on the effects cyanobacterial toxins on copepods, yet these also show high diversity in tolerance to cyanobacteria. The copepods *Acartia bifilosa* and *Eurytemora affinis* from the Baltic Sea offered mixed diets containing *Nodularia* accumulated nodularin, indicating toxin assimilation and uptake, with negative effects on gross growth efficiency (Kozlowsky-Suzuki et al., 2003). In general, calanoid copepods ingest filamentous cyanobacteria such as *Nodularia* (nodularin producer) or *Cylindrospermopis* (cylindrospermopsin producer) with negative, but non-lethal effects, indicating some degree of detoxification (Bouvy et al., 2001; Panosso et al., 2003; Engström-Öst et al., 2015). In contrast, temperate calanoid copepods *Eurytemora affinis* and *Pseudodiaptomus forbesi* ingested lethal doses of *Microcystis* in mixed food diets, causing acute toxicity and indicating inefficient detoxification despite selective grazing on alternative food (Ger et al., 2010a,b). Yet, some copepods select against cyanobacteria but are also tolerant to ingested toxins (DeMott and Moxter, 1991; Reinikainen et al., 2002b). Another recent study found that a tropical copepod from the genus *Notodiaptomus* was immune to the negative effects of ingesting *Microcystis* in diets dominated by a MC-producing strain (Ger and Panosso, 2014). Thus, along with selectivity, detoxification and tolerance to cyanobacterial metabolites might play a major role in the abundance and ecology of copepods (Karjalainen et al., 2007; Ger and Panosso, 2014).

Cyanotoxin detoxification and tolerance in microzooplankton grazers seems common, but poorly understood. Although the ciliate *Nassula* grew on an exclusive diet of a MC-producing *Planktothrix* strain during eight months, short-term feeding trials showed that ciliates offered the MC-producing strain displayed slower growth and increased levels of antioxidant enzymes compared to ciliates fed with non-MC producing strains (Combes et al., 2013). Amoeba isolated from a toxic *Microcystis* bloom grazed differently on two MC-producing *Microcystis* strains due to the release of unknown chemical exudates (Van Wichelen et al., 2010). In contrast, amoebae exposure to protein phosphate inhibitors (MCs and anabaenopeptines produced by *Microcystis* and *Anabaena*, respectively) caused the disruption of cell cytoskeletons followed by increased mortality rates (Urrutia-Cordero et al., 2013). These results suggest that the susceptibility of amoebae to cyanobacterial chemical defenses can vary, likely driven by the local adaptation of amoeba to the ingestion of cyanobacterial toxic metabolites (Van Wichelen et al., 2012). Heterotrophic and mixotrophic flagellates can also degrade cyanobacterial toxins such as MCs (Zhang et al., 2008; Van Donk et al., 2009).

3. Plankton interactions in eutrophic inland waters

As eutrophication shifts the primary producers to toxic, nutritionally poor or inedible forms of cyanobacteria, the ecological consequences depend on the community specific stoichiometric constraints and tolerance traits explained above. Typically, in temperate lakes with relatively short bloom periods, the large generalist *Daphnia* is affected most significantly (Ghadouani et al., 2003) and is replaced by smaller cladocerans or selective copepods during bloom events (Hansson et al., 2007a,b). During longer bloom events, including those observed in tropical waters, copepods and small-bodied cladocerans are the dominant grazers coexisting with cyanobacteria (Bouvy et al., 2001; Lacerot et al., 2013). Moreover, cyanobacterial blooms in estuarine systems, where the zooplankton community is dominated by copepods, are also on the rise (Karjalainen et al., 2007; Ger et al., 2010a). Thus, while most of the literature is about *Daphnia*, the ecological interactions of cyanobacteria-dominated systems appear to be driven mostly by grazers other than *Daphnia*. Summarized below are currently identified ecological interactions regulating the function of bloom-dominated plankton ecosystems (see also Fig. 1).

3.1. Grazer effects on cyanobacteria

Grazing by zooplankton is a major component of top-down strategies aimed at reducing cyanobacterial blooms in eutrophic freshwaters (Jeppesen, 1990). Decades of research have consistently pointed specifically to the importance of large *Daphnia*, rather than total zooplankton biomass, in reducing phytoplankton biomass in eutrophic lakes (Carpenter et al., 1985; Pace, 1984; Sanni and Waervagen, 1990; Sarnelle, 1992; Shapiro, 1990; Vanni et al., 1990). This is due to several attributes *Daphnia* possess, including high per capita grazing potential, wide prey size range, large body size, generalist feeding, and high biomass attained during the warmer months in temperate waters (Brooks and Dodson, 1965; DeMott, 1989; Gliwicz, 1990b; Kreutzer and Lampert, 1999).

Effective control of total phytoplankton biomass requires grazing to be relatively non-selective, otherwise grazers can only suppress particular fractions of the phytoplankton assemblage (Leibold, 1989; Porter, 1977). *Daphnia's* relatively large size enables consumption of some filamentous and colonial cyanobacteria (Epp, 1996; Jarvis et al., 1987), though others report the physical inhibition of the cladoceran grazing apparatus by cyanobacterial morphology (DeMott et al., 2001). Regardless, it is well established that daphnids have the widest diet among the freshwater zooplankton and that *Daphnia's* diet widens with increasing body size (Burns, 1969; DeMott, 1989). Also, despite the fact that mass-specific grazing rates decline with body size, higher maximum biomass achieved by larger zooplankton result in higher total grazing in systems dominated by daphnids (Sterner, 1989). Consequently, among freshwater zooplankton, large *Daphnia* species are expected to have the highest potential to control blooms.

Despite the examples of *Daphnia* preventing cyanobacterial blooms in the absence of planktivory (Sarnelle et al., 2010; Chislock et al., 2013a,b), there is also considerable evidence that *Daphnia* are more negatively affected by cyanobacteria than other zooplankton taxa (Gilbert, 1990; Gliwicz, 1990a; Hawkins and Lampert, 1989; Lampert, 1987; Richman and Dodson, 1983; Webster and Porter, 1978). The latter studies, coupled with the commonly observed negative relationship between *Daphnia* abundance and cyanobacterial dominance in lakes, suggests that cyanobacteria may exacerbate *Daphnia* declines (Ghadouani et al., 2006; Hansson et al., 2007a,b; Sommer et al., 1986).

It should, however, be noted that other factors, such as zooplanktivory (Jeppesen, 1990; Persson et al., 1991), vary in concert with cyanobacterial dominance as lakes are enriched. In temperate lakes, rates of zooplanktivory increase with nutrient enrichment (Jeppesen et al., 2000; Persson et al., 1988), and the dominant zooplanktivorous fish selectively feed on large zooplankton (Gliwicz and Pijanowska, 1989; Mittelbach, 1981). Thus, fish zooplanktivory is considered a major factor leading to *Daphnia* declines with the eutrophication of lakes (Sarnelle, 1993; Jeppesen et al., 2003).

Examples of successful bloom control by *Daphnia* have suggested that results are dependent on the grazers being tolerant

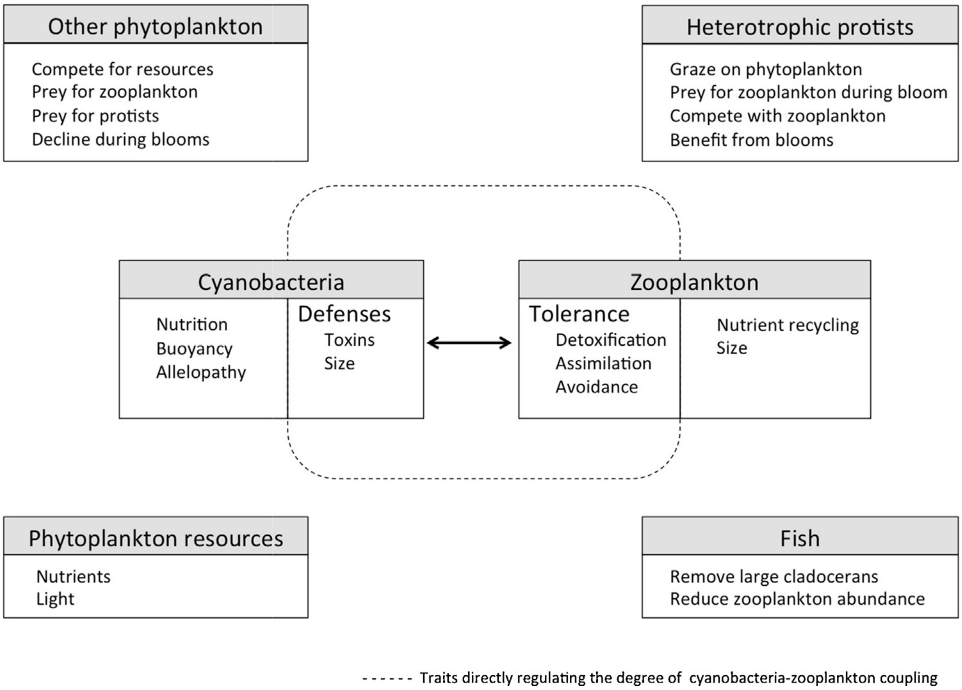

Fig. 1. The planktonic food web in relation to the drivers of cyanobacteria–zooplankton interactions during bloom conditions. The ecological coupling between cyanobacteria and zooplankton, which regulates the function of the plankton ecosystem, depends on the interaction of defensive and tolerance traits of cyanobacteria and zooplankton, respectively (dashed line). Increased cyanobacterial dominance of phytoplankton may shift the species composition and traits of zooplankton, resulting in smaller and selective grazing species, as well as more tolerant genotypes. Blooms also indicate an accumulation of cyanobacteria un-grazed by meso-zooplankton, and an increased role for heterotrophic protists in transmitting primary production carbon and energy to higher trophic levels. Zooplanktivorous fish also reduce the abundance of large *Daphnia*, which further weakens the link between cyanobacteria and zooplankton and may facilitate blooms.

to ingested cyanobacterial toxins, able to grow and reproduce on a diet containing cyanobacteria, and reaching high densities before cyanobacteria begin to dominate phytoplankton (Elser, 1999; Sarnelle, 2007). Recent examples of tolerant *Daphnia* clones in fishless enclosures suggest that control of already established blooms of *Microcystis* is also possible (Chislock et al., 2013a,b). Hence, at least part of the negative relationship between *Daphnia* and cyanobacterial biomass could be attributed to direct grazing effects (but see section 4).

While copepods generally avoid cyanobacterial prey when alternative food is abundant, they are also able to ingest and shorten the filament size of various cyanobacteria (Bouvy et al., 2001; Panosso et al., 2003; Chan et al., 2004). The latter study found that copepods could reduce the ratio of *Anabaena* filaments with heterocysts (thereby reducing the N-fixing capacity), indicating that copepod grazing may also have direct negative effects on cyanobacterial biomass. Reducing filament size also makes cyanobacteria available for smaller grazers like rotifers (Fabbro and Duivenvoorden, 1996). Copepod-dominated zooplankton communities may also facilitate cyanobacteria by preying selectively on the eukaryotic (phytoplankton) competitors of cyanobacteria (Wang et al., 2010; Hong et al., 2013, 2015). If cyanobacterial toxins are used as avoidance cues (Engström et al., 2000; Ger et al., 2011), copepod grazers can be expected to select for increased fitness and ratio of toxin producing cyanobacterial genotypes.

Though most research on zooplankton–cyanobacteria interactions remains skewed toward studies focused on metazoan and crustacean grazers (Ger et al., 2014), protozoan grazers can sporadically dominate zooplankton biomass in lakes and may often account for most of the grazing rates (Pace et al., 1998; Davis et al., 2012). While some authors have associated bloom facilitation to microzooplankton (Porter, 1977; Wang et al., 2010), others have found dramatic suppression of cyanobacterial blooms by free-living amoebae or large ciliates in eutrophic systems (Canter et al., 1990; Van Wichelen et al., 2010). Indeed, protozoa-dominated microzooplankton communities may display similar or even stronger grazing rates on filamentous and colony-forming cyanobacteria than meso- and macrozooplankton herbivores (Davis and Gobler, 2011; Davis et al., 2012). In addition, selective grazing by microzooplankton may potentially regulate the genetic structure of blooms by facilitating certain genotypes without changing total cyanobacterial biomass (Van Wichelen et al., 2010). Still, the use of protozoan grazers to control cyanobacterial blooms remains a controversial topic that cannot be resolved without further understanding of the biotic interactions governing the microbial loop (Dryden and Wright, 1987; Sanders and Wickham, 1993; Sommer et al., 2012).

3.2. Ecological stoichiometry of cyanobacterial blooms

Cyanobacteria may affect key ecosystem properties such as the trophic transfer efficiency of primary production via effects on zooplankton grazers. Cyanobacterial blooms are characterized by low herbivore biomass and altered zooplankton community composition. By reducing the biomass of important planktonic consumers (e.g., *Daphnia*), a lower proportion of primary production is consumed and transferred to higher trophic levels within the food webs. Low nutrition (i.e., FA content) of cyanobacteria limits the growth of *Daphnia* in experimental systems (Müller-Navarra et al., 2000). This effect is likely amplified by low digestibility of and assimilation efficiencies of cyanobacterial carbon created by its poor nutritional quality, which reduces zooplankton gross production efficiencies (Frost et al., 2005). Under traditional ecological paradigms, greater primary production leads to increased grazer biomass and subsequently reduction of prey populations (Molles, 2012). Yet, cyanobacterial blooms are more consistent with recently developed stoichiometrically-explicit predator–prey models (Loladze et al., 2000, 2004), where dilution of the limiting resource due to high prey biomass can reduce the food quality for herbivore consumers, resulting in deterministic predator extinction. Cyanobacterial blooms likely exert a similar constraint on zooplankton consumers by providing a high quantity of food but a low availability of an essential nutrient (e.g., sterols).

Zooplankton-mediated nutrient recycling could also regulate the availability and ratio of dissolved nutrients that control phytoplankton competition (Sterner, 1989), though this depends on a high abundance of elementally unique grazers. The appearance of P-rich *Daphnia* may increase dissolved N:P ratios and alter the type of limitation (from P to N) in the phytoplankton (Elser et al., 1988; Elser and Urabe, 1999). In doing so, this elevated N:P release ratios associated with *Daphnia* could inhibit cyanobacteria, particularly N-fixers, whom appear to be competitively superior under conditions of low N-supply (MacKay and Elser, 1998). Nevertheless, evidence supporting cyanobacterial inhibition via *Daphnia* nutrient recycling is inconclusive, as high N concentrations do not necessarily suppress N-fixing cyanobacteria (Paerl, 2008), and experimental manipulations have not yielded clear and consistent effects (Paterson et al., 2002; Sarnelle, 2007). The net effect of *Daphnia* stoichiometry on cyanobacterial blooms and their formation likely depends on starting conditions (timing of animal appearance vs. bloom formation), the background concentrations of dissolved nutrients relative to the flux emanating from the zooplankton pool, the species of cyanobacteria and their own unique physiological traits, and the environmental and food web context (e.g., depth of lake, presence of predators, etc.). In a recent mesocosm study, a copepod dominated tropical zooplankton community reduced phytoplankton C:P ratios, indicating that selective grazers can also transfer P to N-fixing *Cylindrospermopsis* (Hong et al., 2015).

The production of secondary metabolites (i.e., toxins) may be linked to the nutrient status of the cyanobacteria. If toxins contain the limiting nutrient, cyanobacteria should reduce the production and release of these metabolites unless they contribute to nutrient acquisition and retention (Van de Waal et al., 2014). Indeed, N-limitation can constrain MC production in *Microcystis* presumably because it is relatively N-rich content (Horst et al., 2014). This reduction depends, partly, on the type of MC, which vary in their N content, and on the availability of carbon and/or light (Van de Waal et al., 2009). Greatest MC production has been found under low-light, high carbon and high N environments, conditions where N is least limiting (Van de Waal et al., 2009). These results suggest that N-enrichment of lakes may increase the probability of MC production by alleviating acute N-limitation (Van de Waal et al., 2010, 2014). There appears to be an important role of toxin stoichiometry that is linked to the nutrient-status of cyanobacteria, which should be examined more closely especially for different taxa and toxins.

3.3. Fate of cyanobacterial carbon and energy

Despite the well-documented examples of zooplankton ingesting cyanobacteria, the global trend of increasing blooms indicates that cyanobacteria, when provided sufficient nutrients, routinely outgrow grazing losses at larger spatial and temporal scales. Generally, cyanobacteria are less grazed than most other phytoplankton groups, which may be due to low nutritional value, clogging of herbivore feeding apparatus, and cyanotoxins that reduce the fitness of grazers. It is likely that all of the features mentioned above lead to a weakening of the top-down trophic pressure on cyanobacteria. Notably, the weak link between zooplankton and cyanobacteria is observed even when fish predation is low (Dickman et al., 2008; Rondel et al., 2008; Lacerot et al., 2013; Hansson et al., 2013). While blooms can shift the zooplankton community composition to smaller and more selective grazers (Hansson et al., 2007a,b), zooplankton often attain high biomass during toxic cyanobacterial blooms (Bouvy et al., 2001; Souza et al., 2008; Davis et al., 2012). Although this indicates an alternative source of nutrition for zooplankton during bloom conditions, the ecological fate of un-grazed cyanobacterial biomass is poorly understood.

As eutrophication and un-grazed phytoplankton increases, so does the role of microbial interactions on the transfer of energy to higher trophic levels (Azam et al., 1983; Riemann and Christoffersen, 1993; Pace et al., 1998). A substantial amount of carbon flows through the microbial loop before reaching top-predators (Matveev and Robson, 2014), and detrital carbon sources subsidize food webs via assimilation by bacteria and zooplankton (Pace et al., 2004; Kritzberg et al., 2005). Depending on food conditions, all zooplankton are omnivores to varying degrees, and many metazoan zooplankters preferentially select protozoa over cyanobacteria as a food source in eutrophic systems (Sanders and Wickham, 1993). Fish zooplanktivory further shifts the zooplankton community to smaller species that feed selectively on protozoan populations (Brooks and Dodson, 1965).

Heterotrophic microzooplankton serve as a critical link in the transfer of detrital carbon to larger zooplankton (Sanders and Wickham, 1993), and copepods are known to rely on heterotrophic protists associated with decomposing cyanobacterial detritus for nutrition (Koski et al., 2002). In addition, microzooplankton can synthesize and transfer polyunsaturated fatty acids (PUFA) to higher trophic levels, liberating their growth from the stoichiometric constraints of cyanobacterial prey and upgrading the nutritional quality of cyanobacteria to higher trophic levels (Sanders and Wickham, 1993; Bec et al., 2006). Nevertheless, additional links between primary producers and zooplankton also indicate higher energy loss through respiration (Christoffersen et al., 1990; Pace et al., 2004).

The seasonal biomass of heterotrophic protists in eutrophic temperate systems follows a bimodal pattern with high biomass in spring and summer responding to increases in phytoplankton and associated bacterial densities (Sommer et al., 2012). The role of the microbial loop also increases in warmer waters and toward the equator (Sarmento, 2012). Bacterial production increases with primary production along the trophic gradient, and highly diverse communities coexist with cyanobacterial blooms (Christoffersen et al., 1990; Eiler and Bertilsson, 2004). Davis and Gobler (2011) showed that protozoan dominated microzooplankton assemblages were capable of grazing on both toxic and non-toxic *Microcystis* strains during bloom events. In contrast to microzooplankton, the grazing rates of metazoan zooplankton were negatively correlated with increased abundance of potentially toxic cyanobacteria (*Microcystis*, *Anabaena* and *Cylindrospermopsis*) in that study.

These and other results suggest that a stronger link might emerge between the cyanobacteria-protozoa assemblage than the cyanobacteria-metazoa during bloom conditions (Bouvy et al., 2000; Koski et al., 2002). Depending on the tolerance traits of larger zooplankton, a significant part of the cyanobacterial carbon pool may flow to higher trophic levels via the classic food chain, i.e., direct grazing on cyanobacteria by metazoan zooplankters (Perga et al., 2013; Hogfors et al., 2014). Hence, the links among cyanobacteria, the microbial loop, and crustacean zooplankton merit further study.

4. Rapid evolution among cyanobacteria and zooplankton

Historically, ecologists studying species interactions have assumed that the ecological traits of species are fixed (Chase and Leibold, 2003). Yet, the short generation time of zooplankton and phytoplankton suggests that evolutionary change may occur rapidly and with consequences on ecosystem structure and function (Dam, 2013). Reports of within species variability in zooplankton tolerance traits against toxic phytoplankton are now common from both marine and freshwater systems (Sarnelle and Wilson, 2005; Dam, 2013). Such variation is the raw material of micro-evolution, though information on plankton is scarce.

4.1. Micro-evolutionary dynamics in zooplankton populations

That genotypes within a species vary in their tolerance of toxic cyanobacteria in their diet can be traced back to laboratory experiments by Gilbert (1990), who found that a toxic strain of *Anabaena* reduced the population growth rate of a *Daphnia pulex* clone to near zero while having no effect on another clone. In this case, the two clones may have been sister species (*pulex* vs. *pulicaria*), a taxonomic distinction that was not well established at the time. Subsequently, it has been shown that genotypes within *Daphnia galeata* and *Daphnia pulicaria* vary in tolerance, either over time periods (Hairston et al., 1999, 2001) or across lakes (Sarnelle and Wilson, 2005) that vary in cyanobacterial abundance. Further, there may also be a gradient of response between the average tolerance of *D. pulicaria* and the trophic state of the source lake (Sarnelle and Wilson, 2005). It is now clear that *Daphnia* genotypes isolated from eutrophic habitats are likely to be more tolerant to toxic cyanobacteria than genotypes isolated from oligotrophic habitats (Hairston et al., 2001; Sarnelle and Wilson, 2005).

Initial observations of varying tolerance across habitats have been followed recently by studies showing substantial intraspecific variation in cyanobacteria tolerance in species of both *Daphnia* and *Bosmina* isolated from the same population on the same date (Jiang et al., 2013a,b). In both cases, some genotypes of each species achieved positive population growth rates on a diet consisting of 50% (for *Daphnia*) or 100% (for *Bosmina*) MC-producing *Microcystis* (Jiang et al., 2013a,b). Comparing across the two studies, the greater tolerance of *Bosmina* may help to explain the field observation of higher *Bosmina* success in more eutrophic habitats (Jiang et al., 2013a,b). Local adaptation of marine copepods to the occurrence of dinoflagellate (*Alexandrium*) blooms suggests that improved zooplankton tolerance to toxic phytoplankton is a global phenomenon (Dam, 2013).

Studies on the defensive and offensive adaptations by phytoplankton and zooplankton, respectively, have primarily focused on phenotypic plasticity (Jang et al., 2003; Gustafsson and Hansson, 2004; Gustafsson et al., 2005; Sarnelle and Wilson, 2005; Van Gremberghe et al., 2009a,b). Adaptive trait plasticity can have important ecological ramifications (Pohnert et al., 2007; Van Donk et al., 2011), but does not necessarily lead to micro-evolution in plankton populations. For example, transgenerational adaptations in some cladocerans (Gustafsson et al., 2005; Guo and Xie, 2006; Jiang et al., 2013a,b; Li and Jiang, 2014) have been shown to increase tolerance in zooplankton to toxic cyanobacteria in the diet. Although the molecular mechanisms driving these maternal effects have received some attention (Schwarzenberger et al., 2012, 2014; Lyu et al., 2015), many relevant areas remain unexplored. For example, despite the potential for epigenetics (DNA methylation variation) to influence plankton species interactions (Ho and Burggren, 2010) almost nothing is known regarding the role of epigenetics related to freshwater zooplankton (e.g., heavy metal effects on *Daphnia* epigenetics, Vandegehuchte et al., 2010). There are no relevant epigenetics studies reported on cyanobacteria either, and the role of epigenetics on transgenerational plankton adaptations merits further attention.

4.2. Micro-evolutionary dynamics in cyanobacterial defenses

The genetic machinery for the synthesis of non-ribosomal toxic peptides, such as the microcystin synthetase genes, is of ancestral origin and present in distant lineages of cyanobacteria (Rantala et al., 2004). The fact that cyanobacteria still preserve similar morphologies and non-ribosomal pathways encoding toxic peptides suggest that the evolutionary forces selecting for their maintenance are accordingly high (Agha and Quesada, 2014). The patchy distribution of genes encoding MCs among modern cyanobacterial lineages indicates that some cyanobacteria have lost the ability to produce the toxin throughout their evolutionary history (Rantala et al., 2004). Yet, cyanobacterial strains lacking biosynthesis of MCs may contain genes for the synthesis of a number of other non-ribosomal peptides, many of which potentially provide similar ecological functions (Sivonen and Börner, 2008; Agha and Quesada, 2014). This suggests that modern cyanobacterial populations have been selected evolutionarily toward diversifying through the production of unique assortments of peptides with distinct toxic properties (Agha and Quesada, 2014). Knowledge regarding why toxicity occur in many cyanobacteria is scarce. Toxicity is relatively uncommon among other phytoplankton taxa, though it is well known for some dinoflagellates and diatoms (Pohnert et al., 2007). Whatever the reason for toxicity is, it raises many questions, such as why be toxic? Are the toxins mainly a metabolic by-product, advantageous in competition or the reduction of herbivory and other biotic agents, such as parasitism?

As with many other putative phytoplankton defense chemicals, the ecological and evolutionary role of cyanobacterial toxins including MCs, nodularins, saxitoxins, and cylindrospermopsin is unresolved (Pohnert et al., 2007). In addition to grazer defense, MCs have multiple putative intra- and extra-cellular functions, including attraction of beneficial bacteria, allelopathy against competing phytoplankton, iron chelation and uptake, anti-oxidant properties, and even light harvesting adaptations (Kaebernick and Neilan, 2000; Vardi et al., 2002; Paerl and Otten, 2013; Makower et al., 2015). The synthesis of these non-ribosomal peptides depends on multiple biological, chemical, and physical factors, which limit potential grazer selection for toxin production. Since the evolution of cyanobacterial toxins such as MCs predates eukaryotic grazers (Rantala et al., 2004), the original role of these metabolites is not likely an anti-grazer defense, at least not for crustacean zooplankton. Moreover, given horizontal gene transfer in cyanobacteria, selective forces operating on toxin producing genes such as the *mcy* complex may be overridden (Treangen and Rocha, 2011), likely resulting in weak grazer selection for toxin production in cyanobacteria compared to eukaryotic toxic phytoplankton.

5. Eco-evolutionary implications of increased eutrophication on plankton dynamics

Within-species variation is fundamental for evolution (De Meester, 1996; Hairston et al., 2005; Litchman and Klausmeier, 2008; Stoks et al., 2014), and cyanobacterial and zooplankton species exhibit enormous genetic and phenotypic diversity (Boersma et al., 1999; Lynch et al., 1999; Saker and Neilan, 2001; Wilson et al., 2005; Van Gremberghe et al., 2009a,b). Given their relatively short generation times (i.e., hours to days), plankton communities have become model organisms for theoretical and empirical rapid evolution studies (Hairston et al., 1999, 2001; Yoshida et al., 2003; Lemaire et al., 2011), including those aimed at understanding the consequences of micro-evolution on community structure and ecosystem function (Chislock et al., 2013a,b). Hairston's seminal papers on rapid evolution in a *Daphnia galeata* population in Lake Constance (Hairston et al., 1999, 2001) documented increased tolerance to toxic cyanobacteria during an intense eutrophication period. Interestingly, less cyanobacteria-tolerant *D. galeata* clones returned to the population as Lake Constance became less productive and cyanobacteria were less dominant in the phytoplankton community. Moreover, Sarnelle and Wilson (2005) found that local adaptation in *Daphnia* to toxic cyanobacteria is a more general phenomenon than previously thought, suggesting that clones from eutrophic lakes are generally more tolerant to toxic cyanobacteria than conspecifics collected from oligotrophic lakes. Overall, differences in tolerance measured in laboratory assays can in turn translate into enormous differences in top-down effects in the field (Chislock et al., 2013a).

5.1. Evolutionary trade offs of tolerance

Ecological trade-offs fundamentally influence the value of adaptive induced and constitutive traits in different environments (Yoshida et al., 2004; Yin et al., 2011; Riessen, 2012). Without a functional or physiological cost, beneficial defensive and offensive traits should be commonplace for phytoplankton and zooplankton, respectively. Plankton, however, exhibit large trait variation within and among species (Litchman and Klausmeier, 2008; Litchman et al., 2013). Despite the large literature describing mechanisms associated with ecological interactions between cyanobacteria and zooplankton, the primary focus of most studies has been on cyanobacterial traits, especially their morphology, secondary metabolite chemistry, and nutritional composition (Porter, 1977; Lampert, 1987; Wilson et al., 2006; Tillmanns et al., 2008). Traits associated with tolerance in zooplankton to toxic cyanobacteria in the diet have been attributed to acclimation (Ger et al., 2011), behavioral shifts (Haney and Lampert, 2013), protease inhibitor tolerance (Von Elert et al., 2012; Kuster and Von Elert, 2013), or the molecular mechanisms underlying these and unstudied phenomena (Schwarzenberger et al., 2012, 2014; Lyu et al., 2015). Only few studies have examined the fitness costs associated with evolutionary adaptations between cyanobacteria and zooplankton with a study bias toward consumers observed in laboratory settings (Medina et al., 2007; Haney and Lampert, 2013). To fully understand the long-term implications of cyanobacteria–zooplankton interactions, more studies need to consider the costs and consequences of evolutionary adaptations that mediate cyanobacteria–zooplankton interactions (e.g., co-evolutionary arms race), especially those linking laboratory assays with longer-term field experiments (Chislock et al., 2013a).

5.2. Interspecies vs. intraspecies variation

Large trait differences within species (Hairston et al., 2001; Jiang et al., 2013a,b; Sarnelle and Wilson, 2005; White et al., 2011) have methodological, ecological, and applied implications. In practical terms, the recognition that species traits are variable implies that studies aimed at measuring species differences (interspecific variation) should scale such differences against intraspecific variation rather than against experimental error. For example, variation in the inhibitory effect of toxic *Microcystis* on the population growth rate of different clones of a zooplankter species can be compared with variation within that taxon in general (Wilson et al., 2006). While the range of population growth inhibition between the least and most tolerant genotypes of *Bosmina longirostris* from the Yingtao River was 0.77 effect size units, the standard deviation of cyanobacterial effect was 0.73 for 11 species of cladocerans feeding on toxic cyanobacteria using the effect metric ($n = 177$, Wilson et al., 2006). Thus, intraspecific variation in tolerance for one species of cladoceran collected from one location and feeding on one strain of *Microcystis* is large compared to variation measured for multiple cladocerans from many locations feeding on a variety of toxic cyanobacteria. Hence, it may be misleading to ignore intraspecific variation when making inferences about interspecific trait variation (Chase and Leibold, 2003; Sanford et al., 2003).

5.3. Top down control

The effectiveness of using *Daphnia* to manage cyanobacterial blooms remains a controversial topic due to contrasting examples of both success and failure. On the one hand, cyanobacteria are identified as drivers of phytoplankton escape from *Daphnia* control in fertilization experiments in the absence of fish predation (Brett and Goldman, 1997; Carpenter et al., 1995, 2001; Ghadouani et al., 2003). At the same time, *Daphnia* have been reported to suppress total phytoplankton, including cyanobacteria, in eutrophic lakes when fish predation pressure was relaxed (Chislock et al., 2013a,b; Lynch and Shapiro, 1981; Reinertsen et al., 1990; Sanni and Waervagen, 1990; Sarnelle, 1993; Shapiro and Wright, 1984; Vanni, 1984; Vanni et al., 1990). Such conflicting outcomes from biomanipulation experiments may be a result of evolutionary changes in both *Daphnia* and cyanobacteria selected by increasing eutrophication over decades.

The first line of evidence suggests that only populations of *Daphnia* from lakes with a relatively long history of eutrophication are able to suppress cyanobacteria. A recent study has shown that cyanobacteria tolerant *Daphnia pulicaria* clones suppressed a pre-existing and toxic bloom of cyanobacteria by 95% after 6 weeks, while sensitive (naïve) *D. pulicaria* had no discernable impact on phytoplankton abundance or community structure (Chislock et al., 2013b). Clearly, the influence of grazer traits can be as large as the effect of species presence. Moreover, the results of this experiment imply that any tolerance developed in sensitive *Daphnia* populations via phenotypic plasticity or maternal effects was not sufficient to have any noticeable effect on a cyanobacterial bloom.

That *Daphnia* control of cyanobacteria is more likely in lakes with a history of cyanobacterial blooms is further supported by the mismatch between phytoplankton responses to experimental fertilization of nutrient poor lakes vs. responses to food-web manipulation in eutrophic lakes. For example, there is a positive linear relationship between top-down effects on total phytoplankton biomass and phosphorus enrichment in temperate lakes (Sarnelle, 1992), with large differences in phytoplankton response to enrichment in enclosures and lakes with contrasting trophic structure (Mazumder, 1994; Sarnelle, 1994). Such differences might involve adaptive gradients of toxin-tolerance in *Daphnia* that develop over decades, in response to long-term average exposure to cyanobacterial toxins associated to trophic states. Thus, it is likely that strong experimental fertilization moves a system beyond its long-term average toxicity in a relatively short time such that *Daphnia* cannot adapt via natural selection. In contrast, grazer populations in systems that have been eutrophic for decades may already harbor, via heritable adaptation, a sufficient degree of cyanobacterial tolerance to enable top-down control of toxic blooms (Chislock et al., 2013a,b).

Given future scenarios of increased bloom duration, how long tolerant *Daphnia* may continue to suppress cyanobacteria is a critical question for future research. Following the removal of planktivorous fish, the control of cyanobacteria by *Daphnia* may erode after two to three months (Sarnelle, 2007). The eventual return of zooplanktivorous fish, due to practical limitations, is considered as the main reason why suppression of cyanobacteria by *Daphnia* erodes over time (Hansson et al., 1998). Yet, there may also be concurrent phenotypic or evolutionary changes in cyanobacteria responding to increased grazing pressure, which could also result in the erosion of top-down *Daphnia* control. It is therefore critical to distinguish the effects of adaptive trait variability in cyanobacteria from those due to the fish community in future studies using tolerant *Daphnia* to control cyanobacteria.

5.4. The evolutionary arms race

Cyanobacteria and their grazers have co-occurred, and thereby co-evolved over a long time. The increased intensity and duration of harmful algal blooms selects for improved tolerance traits (genotypes) in zooplankton species may be expected to select for improved defenses in phytoplankton against more tolerant grazers, triggering an evolutionary arms race scenario. That most information comes from temperate climates where pronounced seasonality and short bloom duration (Sarnelle, 1993; Sommer et al., 1986) means that any potential arms race between grazers and cyanobacteria is re-set each winter, with the combatants being pushed back to the starting line. Even within the limited time frame of a temperate-zone summer however, there is some evidence that *Daphnia* suppression of cyanobacteria erodes over time (>2 months, Sarnelle, 2007). Limits for top-down control might involve adaptive chemical defenses by cyanobacteria under strong grazing pressure, though could also result from ecological mechanisms such as benthic refuges that allow colonies to increase in size to the point where they become invulnerable to all grazing (Lynch, 1980). The issue of countermeasures by toxic cyanobacteria warrants further study, but such studies will be most profitable if the cyanobacterial strains used are recent isolates rather than from long-standing culture collections, as the latter often lack important ecological traits found in nature (White et al., 2011).

In contrast to the temperate zone, persistent stratified and warm conditions in tropical lakes (Kilham and Kilham, 1990) likely allow ample time for micro-evolutionary defenses in cyanobacteria. Permanent bloom conditions found in tropical climates frequently co-exist with high zooplankton biomass, indicating that the evolutionary arms scenario may result in a stale mate. This is further supported by the observations of genotype–genotype interactions among *Daphnia* and *Microcystis* strains from various lakes (Lemaire et al., 2011). In that study, clones of *Daphnia* exposed to local strains *Microcystis* from the same lake survived better than *Daphnia* exposed to strains of *Microcystis* from distant lakes, showing that local populations are able to co-evolve in response to each other. In another study, toxin (MC) production did not provide an anti-grazer defense against co-occurring zooplankton populations (Davis and Gobler, 2011). These suggest that clones of herbivores are more sensitive to strains of the cyanobacteria that they have never encountered before than local strains, and the interaction strength between cyanobacteria and zooplankton is dependent on local adaptation of both grazer and prey (Lemaire et al., 2011).

6. Biases and research gaps

Over five decades of research in the field of cyanobacteria–zooplankton interactions has provided significant advancements within plankton ecology, much of which is summarized in this review. As information on the variability in cyanobacteria and their grazers accumulate, important biases and gaps in research emerge. Most of the biases are justified by the fact that research has to start somewhere and then build on what is known. Accordingly, the majority of laboratory and field studies come from northern temperate regions and focus on *Daphnia* and *Microcystis* as the model organisms, with little regard to the history of exposure of these organisms to each other. Below are some of the major current biases and research gaps that emerge from the review of literature (summarized in Table 1).

6.1. *Daphnia*

Most research on the tolerance of freshwater zooplankton to toxic cyanobacteria has focused on the large cladoceran *Daphnia*. Part of this can be attributed to the latitudinal bias in limnology toward temperate environments coupled with *Daphnia* being a largely cold-adapted genus (Fernando, 1994). While this bias can be justified for ecological reasons in temperate freshwaters, there are also practical considerations as *Daphnia* is relatively easy to isolate, culture and use in both laboratory and field experiments. Moreover, *Daphnia* is the only freshwater zooplankter that has been consistently demonstrated to suppress the total phytoplankton biomass (including cyanobacteria) at large spatial and temporal scales (Jeppesen, 1990; Leibold, 1989; Meijer et al., 1999; Sarnelle, 1992). Lastly, large *Daphnia* are a highly-preferred resource for consumers on the next trophic level, such as zooplanktivorous fish (Gliwicz and Pijanowska, 1989; Mittelbach, 1981), making *Daphnia* an important conduit for trophic energy flow, at least in temperate, arctic and high-elevation freshwaters. Yet, during temperate summers, and in warmer, less-seasonal or estuarine environments, *Daphnia* is typically replaced by smaller or selective grazers such as copepods. Consequently, more research is needed on other zooplankton taxa, including copepods and micro-zooplankton, which regularly co-occur with cyanobacterial blooms.

6.2. Microcystis *and microcystins (MCs)*

The study of toxin tolerance in freshwater zooplankton has emphasized one genus of cyanobacteria, *Microcystis*, and to a lesser extent, one class of toxin produced by multiple cyanobacterial genera, the MCs. This bias is reasonably justified by the widespread occurrence of *Microcystis*, its reputation for producing blooms, and the high toxicity associated with such blooms (Chislock et al., 2013a; Reynolds, 1984; Rinta-Kanto et al., 2009). MCs are widely considered to be the most toxic and the most commonly reported of the chemically-described cyanobacterial toxins (Graham et al., 2004; Sarnelle et al., 2010). Recently, research into the effects of another class of toxic peptides, known as protease inhibitors, has also been on the rise (Sadler and Von Elert, 2014a,b), and there are numerous known and likely unknown metabolites produced by cyanobacteria that negatively affect zooplankton fitness or growth, and the bias on only a few of these compounds results in a limited understanding of their effects on zooplankton. Research into the synergistic effects of multiple toxins is also lacking.

6.3. *Use of naïve organisms*

Rapid evolution has important ecological implications for plankton communities. This, however, is a recent insight and the role that local adaptation plays in plankton communities merits further attention. While local adaptation in zooplankton to tolerate cyanobacteria is known, information of local adaptations in cyanobacteria is absent. Despite the literature documenting inducible defenses in cyanobacteria against grazers, including toxic secondary metabolites (Jang et al., 2003, 2007; Pineda-Mendoza et al., 2014), morphology (Van Gremberghe et al., 2009a,b; Yang et al., 2009; Yang and Kong, 2012; Cerbin et al., 2013), and behavior (Christoffersen, 1996, Ferguson et al., 1982; Fialkowska and Pajdak-Stos, 2014), there is a dearth of information documenting grazer-mediated micro-evolution in phytoplankton populations. Given that phytoplankton grow relatively rapidly and the necessary molecular tools exist to track changes in algal genotypes and phenotypes, this area of research is ripe for future work. Experiments on cyanobacteria–zooplankton interactions should consider the exposure history of organisms used.

6.4. *The microbial loop*

The role of the microbial loop and its interactions with the classical food web stands out as a critical research gap. The importance of protozoans is well established in marine and freshwater oligotrophic systems, where phytoplankton biomass is low and zooplankton depend on heterotrophic organisms for food. As eutrophication increases the abundance and dominance of inedible cyanobacteria, the coupling between heterotrophic protozoans and zooplankton also strengthens (Riemann and Christoffersen, 1993; Pace et al., 1998). Thus, the main flux of primary production transfer during blooms likely passes through a variety of heterotrophic protists, including amoebae, ciliates, and flagellates, before reaching zooplankton grazers. The challenge will be to distinguish the intermediary roles of protozoans as both grazers of cyanobacteria and food for larger zooplankton.

6.5. *Tropical vs. temperate systems*

Eutrophic waters in warmer climates experience longer blooms and many tropical lakes and reservoirs exhibit permanent blooms of cyanobacteria throughout the year (e.g. Bouvy et al., 2001). Given the role of cyanobacterial exposure on zooplankton adaptations, it is likely that the selection of tolerance and defensive traits in zooplankton and cyanobacteria, respectively, are accelerated in warmer climates. Moreover, given the future scenarios of climate change, longer blooms are also expected in temperate regions where currently cyanobacterial dominance is limited to weeks or months. Thus, the traits of eutrophic tropical plankton communities may help understand and predict the future of bloom dynamics in temperate regions. For example, most food-web manipulations have been conducted in temperate lakes where seasonality limits the growth season for cyanobacteria to a few summer months, and in such systems successful control of blooms

Table 1
The major biases and research gaps concerning the study of cyanobacteria and their grazers in a more eutrophic world. Each bias corresponds to an associated gap in knowledge, which is covered in this review.

Biases	Gaps
Daphnia based studies	Copepods, rotifers, smaller cladocerans, microzooplankton
Studies with naïve populations	Phenotypic and genotypic plasticity, micro-evolution, co-evolution
Experiments with single cell cyanobacteria	Effects and interactions with colonial and filamentous cyanobacteria
Microcystis and microcystin	Range of other cyanobacteria species and toxins, synergistic effects
Effect of cyanobacteria on zooplankton	Effect of grazers on cyanobacteria defenses and the evolutionary arms race
Focus on crustacean zooplankton and cyanobacteria interactions	Role of microbial loop during blooms
Focus on laboratory or field studies	Linking laboratory and field studies
Temperate climates w/ short bloom duration	Plankton dynamics during longer blooms in warmer climates

only has to last for those few months (e.g., Jeppesen, 1990). Given that prospects for controlling blooms with tolerant *Daphnia* may be limited to a few months, bio-manipulation of longer duration blooms may benefit from looking into tropical systems.

In addition to bloom duration, the structure and function of tropical freshwaters is also different than in temperate regions. For example, large generalist grazers like *Daphnia*, which are key for a strong phytoplankton-zooplankton coupling, are rare in tropical freshwaters (Fernando, 1994). Instead, tropical zooplankton are dominated by smaller and more selective grazers and omnnivorous zooplankton such as copepods, especially in eutrophic waters (Bouvy et al., 2001). Moreover, rates of omnivory increase at all trophic levels in warmer waters including fish (Teixeira-De Mello et al., 2009), though little is known how that affects bloom dynamics (Attayde and Menezes, 2008; Okun et al., 2008). Hence, the dynamics of cyanobacterial blooms and their interaction with zooplankton in warmer climates merit more study.

7. Conclusions

Plankton interactions are dynamic, the number and diversity of organisms involved is large, and the same organisms may have contrasting effects in different lakes due to co-evolution or local adaptation. The interaction of cyanobacterial defenses and zooplankton tolerance traits appear as an underlying mechanism regulating the ecology and management of eutrophic waters, including the stability, toxicity, and control of cyanobacterial dominance. As cyanobacteria blooms continue to expand, the subsequent phenotypic and genotypic selection for zooplankton tolerance and cyanobacterial defenses seems obvious. That eutrophication may select for evolutionary changes in plankton over ecologically relevant time periods prompts challenging questions. The diversity of potential cyanobacterial defense traits and the factors controlling them, along with co-evolutionary dynamics shifting zooplankton tolerance, indicate that future work should focus on isolating the effects of individual factors in controlled laboratory experiments. Another challenge will be to verify the relevance of individual and synergistic mechanisms by scaling up experiments to field conditions. Novel molecular methods allowing the study of gene expression and better-designed field and laboratory experiments to fill the research gaps identified here may provide the necessary tools to understand the eco-evolutionary nature of cyanobacteria–zooplankton interactions.

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