



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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Contents

1. Introduction	129
2. Physiological interactions between cyanobacteria and zooplankton	130
2.1. Traits of cyanobacteria affecting grazers	130
2.1.1. Grazing defenses	130
2.1.2. Nutritional quality of cyanobacteria	130
2.1.3. Phenotypic response of cyanobacteria to grazers (induced defenses)	131
2.2. Zooplankton tolerance traits	132

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2.2.1. Grazing adaptations.	132
2.2.2. Assimilation of toxins and physiological detoxification.	133
3. Plankton interactions in eutrophic inland waters	133
3.1. Grazer effects on cyanobacteria.	134
3.2. Ecological stoichiometry of cyanobacterial blooms.	135
3.3. Fate of cyanobacterial carbon and energy.	135
4. Rapid evolution among cyanobacteria and zooplankton	136
4.1. Micro-evolutionary dynamics in zooplankton populations.	136
4.2. Micro-evolutionary dynamics in cyanobacterial defenses	137
5. Eco-evolutionary implications of increased eutrophication on plankton dynamics	137
5.1. Evolutionary trade offs of tolerance.	137
5.2. Interspecies vs. intraspecies variation	137
5.3. Top down control	138
5.4. The evolutionary arms race	138
6. Biases and research gaps.	138
6.1. <i>Daphnia</i>	139
6.2. <i>Microcystis</i> and microcystins (MCs)	139
6.3. Use of naïve organisms.	139
6.4. The microbial loop	139
6.5. Tropical vs. temperate systems	139
7. Conclusions	140
Acknowledgements	140
References	140

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

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