

Chapter 11

ECOLOGICAL CONTROL OF CYANOBACTERIAL BLOOMS IN FRESHWATER ECOSYSTEMS

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ABSTRACT

Cyanobacterial blooms pose one of the most serious threats to freshwater ecosystems by producing toxic secondary metabolites that can poison aquatic food-webs, pets, livestock, and humans. Consequently, water resource managers routinely employ a variety of strategies aimed at controlling blooms of cyanobacteria, including reducing nutrient inputs, using potent herbicides, disrupting stratification, and shading waterbodies with water-based stains. The role of ecology in cyanobacterial bloom management is poorly understood despite a decades-long history of studies using biomanipulation: the manipulation of higher trophic levels (adding piscivores or removing planktivores) to increase the size, abundance, and grazing pressure of herbivorous zooplankton to reduce algal abundance. Past biomanipulation efforts conducted primarily in temperate systems have provided equivocal results, and the presence of the generalist herbivore, *Daphnia*, seems to be critically important to the success of biomanipulation efforts.

While cyanobacteria are relatively poor quality food for planktonic herbivores including cladocerans, copepods, and rotifers, recent meta-analyses of zooplankton-cyanobacteria studies show that, in general, cyanobacteria can support positive zooplankton population growth and purportedly toxic cyanobacterial secondary metabolites have, if any, ambiguous effects on zooplankton. Furthermore, recent research has shown that freshwater zooplankton, including the cladoceran *Daphnia* and the calanoid copepod *Eudiaptomus*, can adapt to tolerate toxic cyanobacteria in the diet following prolonged exposure to cyanobacterial blooms. Related field experiments clearly show that *Daphnia* can control cyanobacteria when freed from fish predation. In this review, we argue that cyanobacteria may serve as a beneficial food resource for zooplankton, that ecological control of cyanobacterial blooms is practical for some systems, and that greater attention should be placed on direct biomanipulation of zooplankton communities (e.g., stocking *Daphnia*) in conjunction with the manipulation of higher trophic levels. We also highlight the need for more data documenting

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zooplankton-cyanobacteria interactions in tropical freshwater ecosystems, whose biological, chemical, physical, and geological characteristics vary remarkably from their temperate counterparts.

COMMENTARY

Biomanipulation – the alteration of a food-web to restore ecosystem health – has been well-studied in disparate communities [1,2] since the concept was first introduced by Joseph Shapiro and his colleagues as an approach to manage nutrient-rich freshwater lakes [3]. In lakes, the basic premise of biomanipulation is that secondary consumers (planktivorous fishes) are removed either through the addition of tertiary consumers (piscivorous fishes) or harvesting, which allows for the dominance of large-bodied, generalist zooplankton grazers (e.g., *Daphnia*) [4] to control phytoplankton. When planktivorous fishes are abundant and there is no predation refuge (e.g., oxygenated hypolimnion) for large-bodied zooplankton, less efficient small-bodied zooplankton grazers (e.g., rotifers and herbivorous copepods) typically dominate zooplankton communities thus allowing for the overgrowth of phytoplankton (i.e., algal bloom). Many past studies, conducted primarily in temperate systems, have shown strong correlations between the size structure of zooplankton communities and phytoplankton abundance [5-9]. These data support the notion that predatory top-down forces can have important implications for aquatic communities and ecosystems [10,11]. With that said, fish-centric biomanipulation effects on water quality are typically short-lived (i.e., weeks to months), most obvious in small, easily-managed systems (i.e., ponds), and impacted by resource availability, namely phosphorus and nitrogen [12-15]. For example, a common consequence of excess nutrient loading in lakes is elevated primary production [16] and the promotion of algal blooms [17,18]. Given the complexity of algal bloom dynamics across space and time, we still know very little regarding the relative strengths of top-down (predation) and bottom-up (resources) forces regulating ecosystem function in aquatic systems (but see [19,20]). This is especially true for under-studied subtropical and tropical systems [21-23].

Cyanobacteria (blue-green algae) are one of the primary indicators of poor water quality in lentic systems and have been implicated in the sickness and death of pets, livestock, and humans [24,25]. Cyanobacteria tend to dominate algal communities under nutrient enrichment, low nitrogen-to-phosphorus ratios, elevated temperatures, periods of stagnant or stratified conditions, high zooplanktivory, or a combination of these factors [17,26-31]. Regarding food-web interactions, cyanobacteria are considered to be poor food for grazers relative to other algal taxa, such as flagellates and chlorophytes [32,33]. Mechanisms mediating this distinction include the lack of cyanobacterial fatty acids required by zooplankton, colonial and filamentous morphologies, and intracellular toxins produced by several cyanobacterial genera that may negatively affect zooplankton population growth [33-37].

Of these three primary mechanisms, the role of nutritional deficiencies has shown to be the most robust across studies. For example, von Elert and colleagues [36,38-40] have conducted numerous laboratory-based experiments showing that zooplankton somatic and population growth rates can be enhanced when fed cyanobacterial diets supplemented with lipophilic chemical constituents, such as sterols and poly-unsaturated fatty acids, produced by

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some algal taxa (chlorophytes and cryptophytes). Intuitively, large and irregularly-shaped cyanobacterial growth forms (e.g., *Microcystis* colonies or *Anabaena* filaments) should deter grazing by gape-limited zooplankton. However, a recent quantitative literature review of laboratory-based studies showed that filamentous cyanobacteria comprised significantly better diets for freshwater zooplankton relative to diets consisting of single-celled or colonial cyanobacteria [33]. Findings from this meta-analysis may be influenced by the inability of some zooplankton to consume large filaments, thus not ingesting purported intracellular toxins or cyanobacteria lacking essential nutrients. Future experiments should consider using different size fractions of the same phytoplankton diet (i.e., strain) to tease apart the influence of algal size on food quality for zooplankton (see [41,42]). Such an approach would preclude confounding factors related to intra- and interspecific physiological variation in phytoplankton [32,33].

The role of intracellular cyanobacterial secondary metabolites as zooplankton toxins is ambiguous, at best, despite the large zooplankton-cyanobacteria literature. In the same meta-analysis described above, Wilson and colleagues [33] found no clear effects of "toxic" cyanobacteria (defined as cyanobacterial strains shown to produce known toxins, such as microcystin or anatoxin-*a*) on the population growth rates of freshwater cladocerans and rotifers. In other words, zooplankton performed similarly on diets containing toxic or non-toxic cyanobacteria, albeit still worse relative to higher quality diets lacking cyanobacteria. Given that cyanobacteria produce a diverse suite of known and unknown compounds [43,44], it is reasonable to consider that "non-toxic" cyanobacteria (defined as cyanobacterial strains that do not produce known toxins) could produce "toxic" secondary metabolites that are currently unknown. Alternatively, cyanobacterial toxins traditionally identified using bioassays involving rodents may not be toxic to zooplankton. We are aware of only one study which directly tested the effect of one cyanobacterial toxin, microcystin-LR, in the diet on the fitness of a zooplankter, *Daphnia pulicaria* [37]. Data from this study showed that microcystin-LR can be toxic to zooplankton, but that this effect is not universal. For example, one *D. pulicaria* clone isolated from a eutrophic lake that was previously shown to perform well on a diet containing live, toxic *Microcystis* exhibited negative population growth when fed a diet containing lyophilized *Chlorella* (chlorophyte) treated with microcystin-LR. Interestingly, another *D. pulicaria* clone collected from an oligotrophic lake that performed poorly on the same diet containing live *Microcystis* was not affected by microcystin-treated, freeze-dried *Chlorella*. It is unclear what mechanism is driving these patterns, but these data definitely show that *Daphnia* performance on toxin-laced diets were consumer genotype-dependent, albeit not as expected based on their source habitats. Finally, although cyanobacteria are relatively poor food for zooplankton [33], it is imperative to recognize that most zooplankton taxa exhibit positive population growth on diets containing part or all cyanobacteria, regardless of its toxicity or morphology [32], and that the effects of cyanobacteria on zooplankton are likely context specific. Together, these data strongly suggest that the current paradigm describing cyanobacteria as generally harmful to zooplankton may need to be reconsidered.

During cyanobacterial blooms, small-bodied zooplankton tend to dominate plankton communities, and past observational studies have attributed this pattern to anti-herbivore traits of cyanobacteria [35,45,46]. However, planktivorous fish biomass is often positively related to productivity [6]. Thus, alternative explanations for the lack of consumer control of cyanobacteria could include zooplanktivory [47] or synergistic effects of cyanobacterial traits

and consumer control of large-bodied zooplankton [28]. We are unaware of any field empirical tests that have directly studied these hypotheses. Moreover, given that most zooplankton-cyanobacteria studies have been conducted in the laboratory but that the focus of these studies is on dynamics in nature, we encourage a greater emphasis of studies that determine if interactions observed in the laboratory can be extended to the field (see [48]).

Despite strong, but variable, inhibition of *Daphnia* by cyanobacteria in the laboratory, repeated field observations in eutrophic lakes have documented strong suppression of phytoplankton, including cyanobacteria, by *Daphnia* when freed from predation by planktivorous fishes [19,49-52]. Moreover, we have conducted several field experiments of 2-3 months duration (fish-less 144 L enclosures; without or with *Daphnia*) in hypereutrophic aquaculture ponds dominated by various species of cyanobacteria and found consistent, large effects of *Daphnia* on algal abundance (Figure 1, M. Chislock and A. Wilson, unpublished data). One potential explanation for the incongruity between results generated from laboratory and field studies is that laboratory experiments sometimes use *Daphnia* genotypes that are evolutionarily naïve to toxic cyanobacteria or incorporate diets consisting of cyanobacterial genotypes that are especially toxic prey [32,33]. Recent laboratory experiments support this explanation, as *Daphnia* genotypes from eutrophic environments with frequent cyanobacterial blooms are less inhibited by microcystin-producing *Microcystis* than *Daphnia* from oligotrophic environments where cyanobacteria are rare [53,54].

Furthermore, phenotypic acclimation has been observed in *Daphnia* [55], as well as the calanoid copepod *Eudiaptomus gracilis* [56], in response to exposure to sublethal diets of cyanobacteria. Given that some zooplankton can rapidly adapt to tolerate cyanobacteria and their associated toxins, the response of eutrophied systems to abatement efforts may depend not only on the presence of large zooplankton, like *Daphnia*, but also on the role of zooplankton adaptation to cyanobacteria. Available empirical data show that *Daphnia* can suppress cyanobacteria in nature, and *Daphnia* adaptations to toxic cyanobacteria may mediate these interactions. The role of grazer adaptations to better tolerate or avoid harmful prey is under-studied [53-56] but very exciting and could explain some of the variability observed in the zooplankton-cyanobacteria literature [32,33].

While the use of biomanipulation to improve water quality has been well-studied in temperate systems, the potential for top-down control of phytoplankton in subtropical and tropical lakes is less studied (but see [21-23,57]).

Elevated planktivory and temperatures occurring over increased seasonal durations in the tropics can promote cyanobacterial blooms and can extirpate large, competitively superior zooplankton, such as *Daphnia* from lakes [6,28]. It is well-known that species diversity, consumer density, and per capita consumer effects often increase closer to the equator [58-60]. Subtropical and tropical lakes also have more diverse fish communities that are commonly dominated by omnivorous species that consume detritus, phytoplankton, in addition to zooplankton [57].

Consequently, tropical and subtropical communities may be more strongly regulated by complex, web-like species interactions, relative to the chain-like food webs of most temperate lakes [61]. Thus, trophic cascades often documented in temperate lakes may be less common in the tropics. However, this hypothesis is untested, and manipulative field experiments in the tropics are needed to examine the generality of biomanipulation as a tool to improve water quality across systems.

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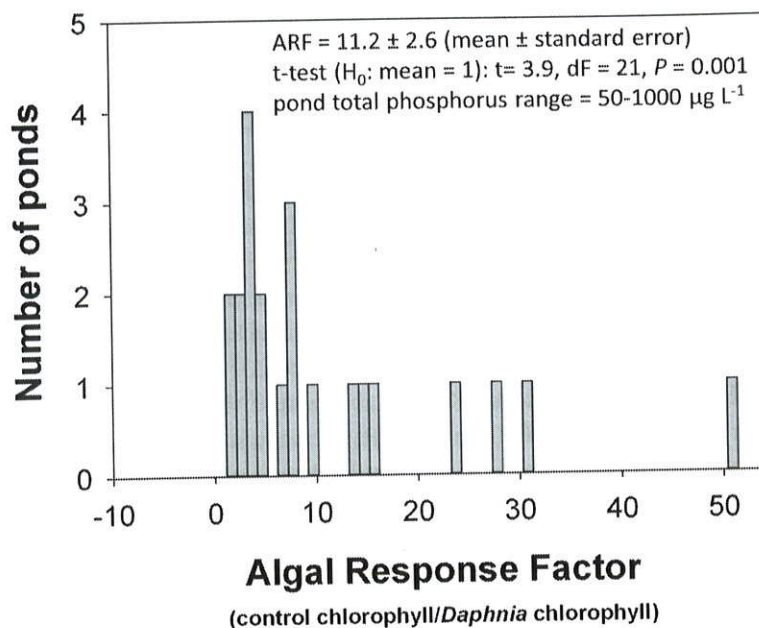


Figure 1. Legend: Histogram of algal response factors (ARF [20]; measured as [(final chlorophyll concentration in control)/(final chlorophyll concentration in treatment)]) in 2-3 months-long field experiments with two treatments (control = no *Daphnia*; treatment = *Daphnia*) conducted in hypereutrophic aquaculture ponds dominated by cyanobacteria (M. Chislock and A. Wilson, unpublished data). An ARF = 1 denotes no difference between final chlorophyll concentrations in the control and treatment. An ARF > 1 shows that the presence of *Daphnia* reduces chlorophyll concentration relative to enclosures lacking *Daphnia* (i.e., control).

Given the influence that predicted climate change and human population growth will have on future water quality and quantity, there is an immediate need by water resource managers to understand how to minimize the intensity and frequency of algal and cyanobacterial blooms. We contend that existing data support the notions that cyanobacteria are not necessarily harmful to zooplankton, that ecological control of cyanobacteria is possible under certain circumstances, and that a more directed focus on the management of large-bodied zooplankton (e.g., *Daphnia*) adapted to cyanobacteria could provide a long-term, sustainable solution to future cyanobacterial blooms in freshwater lakes that contain low densities of planktivorous fishes. We encourage large-scale, field tests of these ideas in the future.

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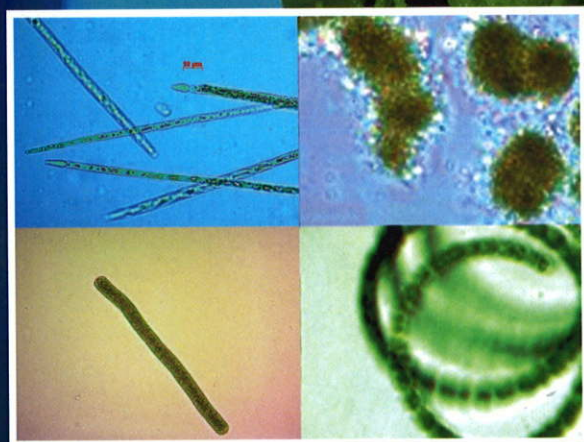
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Ecology, Toxicology and Management



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