Harmful Blooms of Cyanobacteria: Adding Complexity to a Well-Studied Topic

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Cyanobacteria are the oldest phylogenetic group of organisms performing “plant type” (O₂-producing) photosynthesis. They are distributed worldwide in fresh and marine waters and also in some terrestrial habitats. Planktonic cyanobacterial taxa are characterized by a bimodal size distribution with most abundant species either belonging to picoplankton (<2 µm) or forming large colonies [1]. It is the latter group that has received longer and stronger attention by scientists and environmental quality managers due to their predominant role in harmful algal blooms in freshwaters and also partly in brackish inland waters and coastal seas. Cyanobacterial blooms are well established as indicators of environmental degradation [2,3]. The tendency to form surface scums, often associated with a bad odor, makes cyanobacterial blooms more conspicuous to the general public than blooms of other phytoplankton groups.

The relationship of harmful cyanobacterial blooms to environmental degradation is a double-faced one. While being considered to indicate environmental degradation, in particular eutrophication and climate warming, their mass occurrence produces an adverse environment for other aquatic biota and for humans and livestock on the coast. Thus, harmful cyanobacterial blooms are thought to impair ecosystem functioning and ecosystem goods and services, such as fisheries, drinking water production and recreational use of lakes and brackish coastal seas.

It is therefore no surprise that the occurrence, quantification, causal analysis, analysis of effects and search for remedies of cyanobacterial blooms became important topics of research with the onset of broad eutrophication research in the 1970s. Research and monitoring efforts have not ceased since then and were even extended through regulations such as the Water Framework Directive (WFD) of the EU. Cyanobacteria are an essential biological component of phytoplankton water quality assessment, and cyanobacterial biovolume, or their percentage contribution to total phytoplankton biovolume, has been a recommended taxonomic and bloom metric of phytoplankton indices used in ecological status classification schemes by European Member States. However, knowledge gaps during WFD implementation in some cases has resulted in indices that are inconsistent with cyanobacterial ecology. Problems with the indices concern the exclusion of most chroococcalean taxa from cyanobacterial biovolume estimations, erroneous assignments of cyanobacterial species to eutrophic versus oligotrophic waters and the overlooking of deep-water cyanobacterial blooms due to limitations in sampling depth [2,3]. Over almost half a century, an enormous body of knowledge has accumulated: some generalized concepts were crystallized from the body of knowledge, but some of the early generalizations became shaky—or, at least, exceptions have been documented.

In our Special Issue, we have assembled several case studies and three more general articles. The variability of cyanotoxins was examined in the Lakes Prespa system, which has received limited relevant studies despite its global importance for biodiversity [4]. The classic pattern of increasing cyanobacterial biomass and toxin concentration in response to...
an increasing lake trophy was confirmed, and cyanobacterial toxins were also retrieved from carp and pelicans. Dominance shifts between nitrogen-fixing *Dolichospermum* and non-nitrogen-fixing *Microcystis* were analyzed in a 7-year, spatially resolved study in Lake Chaohu, China [5]. *Microcystis* gained dominance at higher temperatures and elevated total phosphorus concentrations, while *Dolichospermum* was favored by lower temperatures and lower total nitrogen levels when temperatures were low. A study of the effect of the cyanotoxin cylindrospermopsin on the macrophyte *Egeria* shows that *Egeria* can tolerate the toxin to some extent and also remove it from the water, pointing at the de-toxifying potential of macrophytes (“green liver”) [6]. Blooms by cyanobacterial picoplankton—usually not notorious bloom formers—are shown to be driven by urea inputs in Sarasota Bay in Florida [7].

The influence of key cyanobacterial traits (buoyancy regulation and nitrogen fixation) on the nutrient reduction threshold for the restoration of cyanobacteria-dominated shallow lakes was analyzed in a model study [8]. While traits of dominant cyanobacteria have little effect on nutrient thresholds during the eutrophication process, they influence the nutrient thresholds for the recovery from the cyanobacteria-dominated turbid to the macrophyte-dominated clear-water state.

A review of the food web relationships of cyanobacteria [9] adds complexity to the traditional view that cyanobacteria are dead ends in food webs, contributing little or nothing to the nutrition of fish and even threatening fisheries by causing fish kills. While there are certainly examples supporting the traditional view, there are counter examples of fish, often cyprinids, coexisting with cyanobacterial blooms and even of fish directly feeding on cyanobacteria.

Similar to the need to add complexity to conventional wisdom about the food web effects of cyanobacteria, some widespread and possibly premature generalizations about the environmental drivers of cyanobacterial blooms also need critical re-examination, with an emphasis placed on case-by-case evaluations of the most promising management options [10]. While global climate change will increase cyanobacteria dominance in many water bodies, there will also be neutral or even negative responses of cyanobacteria depending on chemical, hydrographic and local meteorological conditions, including secondary effects of warming such as storms, changed runoff and water renewal time. The widespread recommendation of a dual-nutrient reduction strategy in order to keep N:P ratios balanced is confronted with the experience that the concentration of P-reductions is often, but not always, more easily achieved, more cost effective and successful while being without harmful side effects. Proposing general rules for the prediction of cyanobacterial toxins is even less possible because of the lack of any uniformity in the response of toxic vs. non-toxic strains of different species to environmental drivers.

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