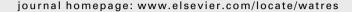


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Climate change: Links to global expansion of harmful cyanobacteria

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ABSTRACT

Cyanobacteria are the Earth's oldest (~3.5 bya) oxygen evolving organisms, and they have had major impacts on shaping our modern-day biosphere. Conversely, biospheric environmental perturbations, including nutrient enrichment and climatic changes (e.g. global warming, hydrologic changes, increased frequencies and intensities of tropical cyclones, more intense and persistent droughts), strongly affect cyanobacterial growth and bloom potentials in freshwater and marine ecosystems. We examined human and climatic controls on harmful (toxic, hypoxia-generating, food web disrupting) bloom-forming cyanobacteria (CyanoHABs) along the freshwater to marine continuum. These changes may act synergistically to promote cyanobacterial dominance and persistence. This synergy is a formidable challenge to water quality, water supply and fisheries managers, because bloom potentials and controls may be altered in response to contemporaneous changes in thermal and hydrologic regimes. In inland waters, hydrologic modifications, including enhanced vertical mixing and, if water supplies permit, increased flushing (reducing residence time) will likely be needed in systems where nutrient input reductions are neither feasible nor possible. Successful control of CyanoHABs by grazers is unlikely except in specific cases. Overall, stricter nutrient management will likely be the most feasible and practical approach to long-term CyanoHAB control in a warmer, stormier and more extreme world.

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1. Introduction

Cyanobacteria (blue-green algae) are the Earth's oldest known oxygen-producing organisms, with fossil remains dating back ~3.5 billion years (Schopf, 2000). Cyanobacterial proliferation during the Precambrian period is largely responsible for the modern-day, oxygen-enriched atmosphere, and subsequent evolution of higher plant and animal life (Schopf, 2000; Whitton and Potts, 2000). This long evolutionary history has served cyanobacteria well, for it has

enabled them to develop diverse and highly effective ecophysiological adaptations and strategies for ensuring survival and dominance in aquatic environments undergoing natural and human-induced environmental change (Hallock, 2005; Huisman et al., 2005; Paerl and Fulton, 2006; Paul, 2008). Today, they enjoy a remarkably broad geographic distribution, ranging from polar to tropical regions in northern and southern hemispheres, where they are capable of dominating planktonic and benthic primary production in diverse habitats.

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As a "microalgal" group, the cyanobacteria exhibit highly efficient nutrient (N, P, Fe and trace metal) uptake and storage capabilities, and they are the only oxygenic phototrophs capable of utilizing atmospheric dinitrogen (N2) as a nitrogen source to support growth via N2 fixation (Fogg, 1969; Gallon, 1992). Furthermore, many planktonic genera are capable of rapid vertical migration by altering their buoyancy, allowing them to exploit deeper, nutrient-rich waters while also taking advantage of radiant-rich conditions near the surface (Ibelings et al., 1991; Walsby et al., 1997; Reynolds, 2006). Lastly, some genera have formed symbioses (as endosymbionts) in diatoms, sponges, corals, lichens, ferns, and mutualistic associations with a variety of other organisms which provide protection and enhance nutrient cycling and availability in nutrient-deplete waters (Paerl and Pinckney, 1996; Carpenter, 2002; Rai et al., 2002).

Over the past several centuries, human nutrient overenrichment (particularly nitrogen and phosphorus) associated with urban, agricultural and industrial development, has promoted accelerated rates of primary production, or eutrophication. Eutrophication favors periodic proliferation and dominance of harmful blooms of cyanobacteria (CyanoHABs), both in planktonic (Fogg, 1969; Steinberg and Hartmann, 1988; Huisman et al., 2005; Paerl and Fulton, 2006) and benthic (Baker et al., 2001; Dasey et al., 2005; Wood et al., 2006; Izaguirre et al., 2007; Elmetri and Bell, 2004; Albert et al., 2005; Ahern et al., 2007; Paerl et al., 2008) environments.

In freshwater ecosystems, P availability has traditionally been viewed as a key factor limiting CyanoHAB proliferation (Schindler, 1975; Schindler et al., 2008), and excess P (relative to N) loading has been identified as favoring CyanoHABs (Smith, 1983; Watson et al., 1997; Downing et al., 2001). The emphasis on P controls is based on the N2 fixing capabilities of some CyanoHAB genera, which help satisfy cellular Nrequirements under P-limited conditions (Paerl and Fulton, 2006). However, at the ecosystem level, only a fraction, usually far less than 50%, of primary and secondary production demands are met by N2 fixation, even when P supplies are sufficient (Howarth et al., 1988; Lewis and Wurtsbaugh, 2008; Paerl and Scott, 2010). Hence, N2 fixation appears to be controlled by factors in addition to P availability. Nutrient loading dynamics have changed substantially over the past several decades. While P reductions have been actively pursued, human population growth in watersheds has been paralleled by increased N loading, often at higher rates than P (Vitousek et al., 1997; Paerl and Scott, 2010). Excessive N loads are now as large a concern as P loads as stimulants of freshwater, estuarine and marine eutrophication and harmful algal (including cyanobacterial) blooms (Conley et al., 2009; Paerl, 2009; Ahn et al., 2011).

Mass development of CyanoHABs, increases turbidity and hence restricts light penetration in affected ecosystems (Figs. 1 and 2). This, in turn, suppresses the establishment and growth of aquatic macrophytes and benthic microalgae and



Fig. 1 — Examples of freshwater systems impacted by proliferating CyanoHABs Upper left, MODIS satellite image of surface cyanobacterial blooms in Lake Erie (US-Canadian Great Lakes) during July, 2007. (Courtesy of NASA and Coastwatch-Great Lakes). Upper right, Cyanobacterial (Aphanizomenon flos aquae) bloom on Lake Dianchi, Yunan Provice, China, July 2006 (Courtesy of http://4.bp.blogspot.com/_KbJGi-TtEtQ/SVGUNroO4aI/AAAAAAAAAE/iGR9zvvSrPg/s400/Dianchi+Lake_China_Blue+Green+Algae+Bloom). Lower left, Cyanobacterial (Microcystis spp.) bloom in Lake Taihu, Jiangsu Province, China, photographed by author H. Paerl during a lake-wide bloom in July, 2007. Lower right, a CyanoHAB bloom (Microcystis and Anabaena spp.) on the lower St. Johns River, Florida during summer, 2005 (Courtesy of Bill Yates/CYPIX).

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