Harmful Algae 14 (2012) 313–334

Contents lists available at SciVerse ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal

The rise of harmful cyanobacteria blooms: The potential roles of eutrophication and climate change

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ARTICLE INFO

Article history:
Available online 29 October 2011

Keywords:
Climate change
Cyanobacteria
CyanoHABs
Eutrophication
Harmful algae blooms
Toxins

ABSTRACT

Cyanobacteria are the most ancient phytoplankton on the planet and form harmful algal blooms in freshwater, estuarine, and marine ecosystems. Recent research suggests that eutrophication and climate change are two processes that may promote the proliferation and expansion of cyanobacterial harmful algal blooms. In this review, we specifically examine the relationships between eutrophication, climate change and representative cyanobacterial genera from freshwater (*Microcystis*, *Anabaena*, *Cylindrospermopsis*), estuarine (*Nodularia*, *Aphanizomenon*), and marine ecosystems (*Lyngbya*, *Synechococcus*, *Trichodesmium*). Commonalities among cyanobacterial genera include being highly competitive for low concentrations of inorganic P (DIP) and the ability to acquire organic P compounds. Both diazotrophic (= nitrogen (N_2) fixers) and non-diazotrophic cyanobacteria display great flexibility in the N sources they exploit to form blooms. Hence, while some cyanobacterial blooms are associated with eutrophication, several form blooms when concentrations of inorganic N and P are low. Cyanobacteria dominate phytoplankton assemblages under higher temperatures due to both physiological (e.g. more rapid growth) and physical factors (e.g. enhanced stratification), with individual species showing different temperature optima. Significantly less is known regarding how increasing carbon dioxide (CO_2) concentrations will affect cyanobacteria, although some evidence suggests several genera of cyanobacteria are well-suited to bloom under low concentrations of CO_2. While the interactive effects of future eutrophication and climate change on harmful cyanobacterial blooms are complex, much of the current knowledge suggests these processes are likely to enhance the magnitude and frequency of these events.

1. Introduction

While cyanobacterial harmful algal blooms have been reported in the scientific literature for more than 130 years (Francis, 1878), in recent decades, the incidence and intensity of these blooms, as well as economic loss associated with these events has increased in both fresh and marine waters (Chorus and Bartram, 1999; Carmichael, 2001, 2008; Hudnell, 2008; Heisler et al., 2008; Hoagland et al., 2002; Paerl, 2008; Paul, 2008; Paerl and Huisman, 2008). Recently, there have been discoveries of previously unidentified cyanobacterial toxins, such as amino β-methylamino-L-alanine (BMAA), and of new genera of cyanobacteria capable of producing previously described toxins (Cox et al., 2003, 2005, 2009; Cox, 2009; Brand, 2009; Kerbrat et al., 2011). To date, factors identified as contributing towards the global expansion of harmful cyanobacterial blooms have included increased nutrient inputs, the transport of cells or cysts via anthropogenic activities, and increased aquaculture production and/or overfishing that alters food webs and may permit harmful species to dominate algal communities (GEOHAB, 2001; HARRNESS, 2005; Heisler et al., 2008). It has also been shown that an increase in surface water temperatures due to changing global climate could play a role in the proliferation of cyanobacterial blooms (Peperzak, 2003; Paerl and Huisman, 2008; Paul, 2008). Importantly, there is consensus that harmful algal blooms are complex events, typically not caused by a single environmental driver but rather multiple factors occurring simultaneously (Heisler et al., 2008). Finally, an improved ability to detect and monitor harmful cyanobacterial blooms, and their toxins as well as increased scientific and public awareness of these events has also led to better documentation of these events (GEOHAB, 2001; HARRNESS, 2005; Sivonen and Börner, 2008).

There have been several reviews of the intensification and global expansion of harmful cyanobacterial blooms in terms of

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doi:10.1016/j.hal.2011.10.027

both abundance, geographic extent, and effects on ecosystem health, as well as factors that may be facilitating this expansion (Paerl, 1988, 1997; Paerl and Millie, 1996; Soranno, 1997; Carmichael, 2001; Saker and Griffiths, 2001; Landsberg, 2002; Codd et al., 2005a,b; Huisman and Hulot, 2005; see multiple papers in Hudnell, 2008). The purpose of this review is to: (1) Highlight important findings of the last decade of harmful cyanobacterial bloom research in fresh, estuarine and marine environments; and (2) Describe how factors associated with eutrophication and climate change affect some of the most widely studied harmful cyanobacterial bloom genera.

2. Background

Cyanobacteria are prokaryotes but have historically been grouped with eukaryotic "algae" and at varying times have been referred to as: blue–greens, blue–green algae, *Myxophyceae*, *Cyanophyceae* and *Cyanophyta* (Carmichael, 2008). More recently cyanobacteria that form harmful blooms have been termed "CyanoHABs" (Carmichael, 2001, 2008; Paerl, 2008) or "cyanobacterial blooms" (Hudnell et al., 2008).

2.1. Toxins

Many genera of cyanobacteria are known to produce a wide variety of toxins and bioactive compounds, which are secondary metabolites (i.e. compounds not essential to the cyanobacteria for growth or its own metabolism) (Sivonen and Jones, 1999). Toxins generally refer to compounds that cause animal and human poisonings or health risks, and bioactive compounds refer to compounds that can have antimicrobial and cytotoxic properties and are often of interest in pharmaceutical and as research tools (Codd et al., 2005a,b). While many of these compounds have recognized toxic effects, the impact and long term effects of many of these compounds is unknown (Tonk, 2007).

Hepatotoxins are globally the most prevalent cyanobacterial toxins followed by neurotoxins (Sivonen and Jones, 1999; Klisch and Häder, 2008; Sivonen and Börner, 2008). Hepatotoxins include: (1) microcystins, (2) nodularins, and (3) cylindrospermopsins. The three most commonly produced types of cyanobacterial neurotoxins are: (1) anatoxin-a, (2) anatoxin-a (S), and (3) saxitoxins. As noted above, Cox et al. (2003, 2005) recently described the presence of the neurotoxic compound, BMAA in nearly all cyanobacteria they tested (Table 1). It has been hypothesized that BMAA may be a possible cause of the amyotrophic lateral sclerosis parkinsonism–dementia complex (ALS-PDC; Cox et al., 2003, 2009; Murch et al., 2004; Cox, 2009). As such, the discovery that this compound is potentially produced by a broad range of cyanobacteria greatly increases the potential for human exposure (Sivonen and Börner, 2008; Brand, 2009). Indeed, in the Baltic Sea, an ecosystem whose primary production is dominated by cyanobacteria, BMAA has been measured in significant quantities in both fish and shellfish (Jonasson et al., 2010).

2.2. Nutrients

Of all of the potential environmental drivers behind harmful algal and cyanobacterial blooms, the one that has received the most attention among the global scientific community has been anthropogenic nutrient pollution. Research indicates that cultural eutrophication associated with the increased global human population has stimulated the occurrences of harmful algal blooms (Anderson, 1989; Hallegraeff, 1993; Burkholder, 1998; Anderson et al., 2002; Glibert et al., 2005; Glibert and Burkholder, 2006; Heisler et al., 2008). As bodies of freshwater become enriched in nutrients, especially phosphorus (P), there is often a shift in the phytoplankton community towards dominance by cyanobacteria (Smith, 1986; Trimbee and Prepas, 1987; Watson et al., 1997; Paerl and Huisman, 2009). Examples of these changes are the dense blooms often found in newly eutrophied lakes, reservoirs, and rivers previously devoid of these events (Fogg, 1969; Reynolds and Walsby, 1975; Reynolds, 1987; Paerl, 1988, 1997). Empirical models predict that in temperate ecosystems, summer phytoplankton communities will be potentially dominated by cyanobacteria at total phosphorus (TP) concentrations of ~100–1000 $\mu g\,L^{-1}$ (Trimbee and Prepas, 1987; Jensen et al., 1994; Watson et al., 1997; Downing et al., 2001).

One reason that P often controls the proliferation of freshwater ecosystems is that many cyanobacteria that bloom in warm waters have the ability to fix nitrogen (N; Paerl, 1988; Paerl et al., 2001). Since many of the bloom forming cyanobacteria genera are not diazotrophic and the proliferation of some blooms may be limited by N (Gobler et al., 2007; Davis et al., 2010), it has been hypothesized both N and P may control harmful cyanobacterial blooms (Paerl et al., 2008; Paerl and Huisman, 2009). While research on cyanobacterial blooms has traditionally considered inorganic N and P pools as being accessed by cyanobacteria or total N and P pools for understanding the trophic state of ecosystems, recent research has demonstrated that organic N and P may be important nutrient sources for cyanobacteria. Much of the soluble N and P pools in most aquatic environments are comprised of organic compounds (Franko and Heath, 1979; Seitzinger and Sanders, 1997; Kolowith et al., 2001) and many cyanobacteria can utilize various forms of dissolved and particulate organic N and P (Glibert and Bronk, 1994; Paerl, 1988; Paerl and Millie, 1996; Pinckney et al., 1997; Berman and Chava, 1999; Glibert and O'Neil, 1999; Davis et al., 2010). Since neither inorganic nutrient pools nor nutrients ratios typically are able to sufficiently explain the extended duration of dense cyanobacterial blooms (Heisler et al.,

Table 1
Major cyanobacterial bloom toxins.

Toxin group	Primary target organ in mammals	Cyanobactrial genera
Microcystins	Liver	*Microcystis*, *Anabaena*, *Planktothrix (Oscillatoria)*, *Nostoc*, *Hapalosiphon*, *Anabaenopsis*, *Trichodesmium*, *Synechococcus*, *Snowella*
Nodularian	Liver	*Nodularia*
Cylindrospermopsin	Liver	*Cylindrospermopsis*, *Umezakia*, *Aphanizomenon*, *Lyngbya*, *Raphidiopsis*, *Anabaena*
Anatoxin-a	Nerve synapse	*Anabaena*, *Planktothrix (Oscillatoria)*, *Aphanizomenon*, *Phormidium*, *Rhaphidiopsis*
Anatoxin-a(S)	Nerve synapse	*Anabaena*
Saxitoxins	Nerve axons	*Anabaena*, *Planktothrix (Oscillatoria)*, *Aphanizomenon*, *Lyngbya*, *Cylindrospermopsis*, *Scytonema*
Palytoxins	Nerve axons	*Trichodesmium*
Aplysiatoxins	Skin	*Lyngbya*, *Schizothrix*, *Planktothrix (Oscillatoria)*
Lyngbyatoxin-a	Skin, gatro-intestinal tract	*Lyngbya*
Lipopolysaccharides	Irritant; affects exposed tissue	All
BMAA	Nerve synapse	All

Sources: Chorus and Bartram (1999), Li et al. (2001a), Codd et al. (2005a,b), Humpage (2008), Klisch and Häder (2008), Smith et al. (2011).