

Chapter 10: Nutrient and other environmental controls of harmful cyanobacterial blooms along the freshwater–marine continuum

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Abstract

Nutrient and hydrologic conditions strongly influence harmful planktonic and benthic cyanobacterial bloom (CHAB) dynamics in aquatic ecosystems ranging from streams and lakes to coastal ecosystems. Urbanization, agricultural and industrial development have led to increased nitrogen (N) and phosphorus (P) discharge, which affect CHAB potentials of receiving waters. The amounts, proportions and chemical composition of N and P sources can influence the composition, magnitude and duration of blooms. This, in turn, has ramifications for food web dynamics (toxic or inedible CHABs), nutrient and oxygen cycling and nutrient budgets. Some CHABs are capable of N₂ fixation, a process that can influence N availability and budgets. Certain invasive N₂ fixing taxa (e.g., *Cylindrospermopsis*, *Lyngbya*) also effectively compete for fixed N during spring, N-enriched runoff periods, while they use N₂ fixation to supplant their N needs during N-deplete summer months. Control of these taxa is strongly dependent on P supply. However, additional factors, such as molar N:P supply ratios, organic matter availability, light attenuation, freshwater discharge, flushing rates (residence time) and water column stability play interactive roles in determining CHAB composition (i.e. N₂ fixing vs. non-N₂ fixing taxa) and biomass. Bloom potentials of nutrient-impacted waters are sensitive to water residence (or flushing) time, temperatures (preference for >15 °C), vertical mixing and turbidity. These physical forcing features can control absolute growth rates of bloom taxa. Human activities may affect “bottom

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up” physical–chemical modulators either directly, by controlling hydrologic, nutrient, sediment and toxic discharges, or indirectly, by influencing climate. Control and management of cyanobacterial and other phytoplankton blooms invariably includes nutrient input constraints, most often focused on N and/or P. While single nutrient input constraints may be effective in some water bodies, dual N and P input reductions are usually required for effective long–term control and management of blooms. In some systems where hydrologic manipulations (i.e., plentiful water supplies) are possible, reducing the water residence time by flushing and artificial mixing (along with nutrient input constraints) can be effective alternatives. Blooms that are not readily consumed and transferred up the food web will form a relatively large proportion of sedimented organic matter. This, in turn, will exacerbate sediment oxygen demand, and enhance the potential for oxygen depletion and release of nutrients back to the water column. This scenario is particularly problematic in long–residence time (i.e., months) systems, where blooms may exert a strong positive feedback on future events. Implications of these scenarios and the confounding issues of climatic (hydrologic) variability, including droughts, tropical storms, hurricanes and floods, will be discussed in the context of developing effective CHAB control strategies along the freshwater–marine continuum.

Introduction

CHABs and Eutrophication

The accumulation of cyanobacterial biomass as bright green, yellow–brown and red blooms in fresh, brackish or saline waters is one of the most obvious and problematic symptom of anthropogenic nutrient enrichment, or eutrophication (Fogg 1969, Reynolds and Walsby 1975, Paerl 1988) (Fig. 1). Cyanobacterial blooms, which often culminate in an unsightly, odoriferous mess, can also cause harm from ecological and health perspectives. Ecologically, blooms may be inedible or toxic to consumer species, causing food web alterations, with potentially detrimental effects on nutrient cycling, biodiversity and fisheries (Fogg 1969, Paerl et al. 2001). Because they may not be consumed, blooms can accumulate as thick scums and mats, which when decomposed cause excessive oxygen consumption (hypoxia), a major factor in the decline or elimination of fish, shellfish, invertebrate and plant habitats (Diaz and Solow 1999). In addition, N₂ fixing cyanobacterial blooms can constitute significant sources of “new” nitrogen

(N), potentially impacting N-driven eutrophication and N cycling (Horne 1977, Paerl 1988). From animal and human health perspectives, blooms produce a variety of odor and taste compounds (geosmins, DMIB), rendering affected waters unsuitable for drinking, swimming and other recreational purposes. Lastly, numerous cyanobacterial bloom species (Fig. 2) produce alkaloid, peptide and other compounds that can be toxic upon ingestion or contact with affected waters (Codd and Bell 1996, Carmichael 1997, Chorus and Bartram 1999).

From research and management perspectives, identifying environmental factors causing and sustaining harmful cyanobacterial blooms (CHABs) is key to developing an understanding of how to control these unwanted manifestations of man-made nutrient, sediment and hydrologic alterations. Cyanobacterial blooms have accompanied human modification of watersheds for agricultural, urban and industrial development for centuries. One line of evidence is the paintings of Holland's agricultural landscapes by the 17th century Dutch Masters, which show surface algal scums diagnostic of nutrient over-enrichment (Fig. 3).



Fig. 1. Harmful cyanobacterial blooms in a range of nutrient-enriched aquatic ecosystems. Upper left. A bloom of the non-N₂ fixing genera *Microcystis aeruginosa* and *Oscillatoria* sp. in the Neuse River, NC (Photo, H. Paerl). Upper right. A mixed *Microcystis* sp. and *Anabaena* spp. (N₂ fixers) bloom in the St. Johns River, Florida (Photo, J. Burns). Lower left. A bloom of the benthic filamentous N₂ fixer *Lyngbya wollei* in Ichetucknee Springs, Florida (Photo H. Paerl). Lower right. A massive bloom of *Microcystis* sp. and *Anabaena* spp. in Lake Ponchartrain, Louisiana (Photo J. Burns).

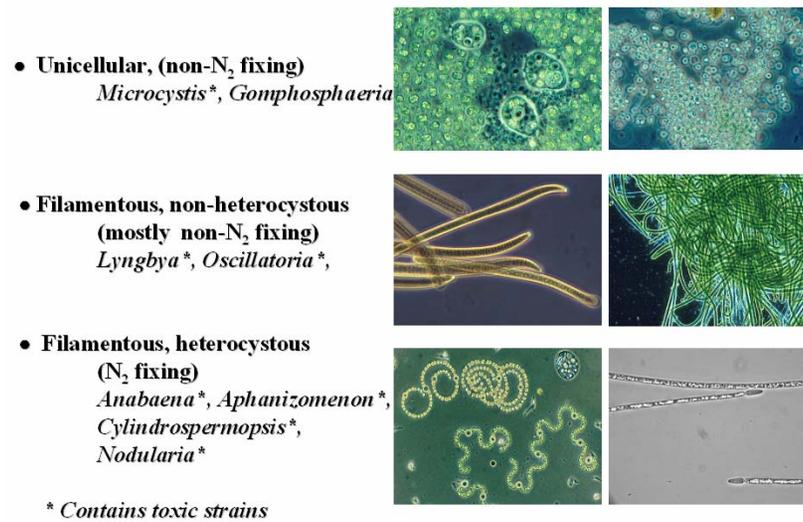


Fig. 2. Photomicrographs of genera representing the three major CHAB morphological groups, including coccoid, filamentous non-heterocystous and filamentous heterocystous types.



Fig. 3. Painting of Haarlemmermeer, a shallow, eutrophic lake in the Netherlands. Jan van Gooyen, ca. 1650. Note the surface scums characterizing the lake.

Nutrients and Hydrology: Key Controls of CHABs

Among the nutrient elements required for aquatic plant growth, N and phosphorus (P) are often most stimulatory, because requirements are high relative to availability. It follows that N and P enrichment are often most effective in stimulating and supporting blooms in receiving waters (Fogg 1969, Reynolds and Walsby 1975). These elements have, and continue to be, the focus of efforts aimed at controlling blooms (Likens 1972, Schindler 1975, Shapiro 1990). While N and P are generally considered the main “culprits” of freshwater and marine eutrophication, they are by no means the *only* environmental factors controlling bloom formation, duration and proliferation. Other natural and anthropogenically–influenced factors also play roles in controlling bloom dynamics. These include; 1) sedimentation which can alter both the nutrient and light environments, and 2) hydrology, specifically freshwater discharge, flushing and residence time, which affect both nutrient delivery to and cycling in affected waters. Nutrient inputs or loads may synergistically or antagonistically interact with sedimentation, freshwater discharge and water column stability (vertical mixing regime) to determine; 1) if a specific water body is susceptible to CHAB formation, 2) the extent (magnitude, duration) to which CHABs may dominate planktonic and or benthic habitats, and, 3) whether an affected water body is amenable to management steps aimed at minimizing or eliminating CHABs (Fig. 4). Here, I will discuss the roles N and P play as nutrients controlling planktonic and benthic CHABs, and the interactive roles light, hydrologic and hydrodynamic conditions play in modulating CHABs. Finally, nutrient and other management options for controlling CHABs will be explored.

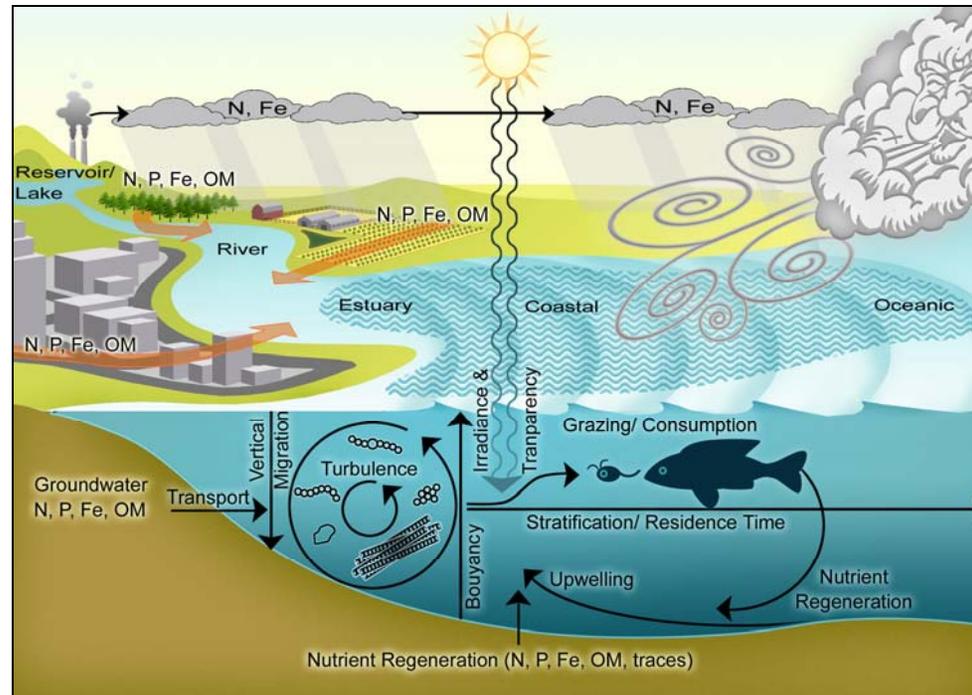


Fig. 4. Conceptual diagram, showing the interactive physical, chemical and biotic controls of cyanobacterial blooms along the freshwater–marine continuum.

Nitrogen and Phosphorus: Linking Their Inputs to CHAB Dynamics

In freshwater ecosystems, excessive P loading has been most frequently linked to eutrophication (Likens 1972, Paerl 1988). P-driven eutrophication can be a prerequisite to N₂-fixing or non-N₂ fixing CHABs. This is often exacerbated by low freshwater discharge (low flushing rates, long residence time), elevated water temperatures >20°C, and strong vertical stratification (Fogg 1969, Reynolds and Walsby 1975, Paerl 1988, Shapiro 1990). In some instances, organic matter-enriched conditions may also favor the CHAB dominance (Pearsall 1932, Fogg 1969). Whether or not N₂ fixers dominate depends on several co-occurring factors, the most important of which is the availability of biologically utilizable N relative to P (Paerl 1990). Freshwater systems having low molar ratios of both total and soluble (biologically-available) N to P (<15) are most likely to experience cyanobacterial dominance (Smith 1983, 1990). Conversely, waters having molar N:P ratios in excess of 20 are more likely to be dominated by eukaryotic algal taxa (Smith 1983). This rule has proven broadly applicable to periodically stratified, long residence (> 30 days) temperate and tropical freshwater systems (Downing et al. 2001).

There are exceptions to the N:P rule. These include; 1) systems in which both N and P loadings are very large (i.e., hypereutrophic systems in which N and P inputs exceed the assimilative capacity of the phytoplankton), and 2) highly-flushed, short residence time systems, in which the flushing rate exceeds growth or doubling rates of cyanobacteria (generally >1 d⁻¹). In N and P enriched systems, N:P ratios may readily exceed 20, but since both N and P are being supplied at close to non-limiting rates, factors other than nutrient limitation (e.g., light, vertical mixing, residence time, salinity, organic matter content) may control algal community activity, biomass and composition. Under these conditions, N₂ fixation confers little if any advantage, and non-N₂ fixing taxa predominate. Often, these conditions favor high rates of primary production and biomass accumulation. This may severely reduce clarity, restricting transmittance of photosynthetically-active radiation (PAR; 400–700 nm), providing a niche for buoyant, surface-dwelling, “nutriphilic” phytoplankton, most notably the bloom-forming non-N₂ fixing cyanobacterial genus *Microcystis*. *Microcystis* and other non-diazotrophic nuisance genera (*Oscillatoria*, some *Lyngbya* and *Planktothrix* species) often co-dominate under these conditions.

Moderately N and P-enriched waters tend to support mixed assemblages of diazotrophic and non-diazotrophic species. This condition often occurs in systems receiving sequential pulse loadings of either high N or P. One scenario is springtime elevated N-laden surface runoff, which favors the establishment of non-diazotrophic bloom species. During summer, when runoff subsides, externally-supplied P loads (from point sources such as wastewater treatment plants, municipal and industrial sources) or internally-generated P loads released from hypoxic sediments, tend to become more prominent components of nutrient loading. P enrichment (i.e., declining N:P ratios) frequently selects for the establishment of N₂ fixing species (Paerl 1982, 1988) (Fig. 5). Once N₂ fixers are established, non-diazotrophic species can remain a significant fraction of the phytoplankton, because they are able to utilize fixed N produced and released by N₂ fixing species (Paerl 1990). Co-existing diazotrophic and N-requiring bloom species are capable of buoyancy regulation, and thus a near-surface existence, in highly productive, turbid waters. Typically, *Anabaena*, *Aphanizomenon* and *Microcystis* (the notorious trio, “Annie, Fannie and Mike”) co-occur under these circumstances. In clearer waters where light reaches the bottom, benthic N₂ fixing and non-fixing assemblages (e.g., *Lyngbya*, some *Oscillatoria*, *Microcoleus*, *Scytonema*, *Phormidium*) can predominate. Mixed assemblages often persist as a bloom “consortium” during summer and fall (Paerl 1983, 1986, 1987), until unfavorable physical conditions such as cooling (<15°C) and water column turnover take place.

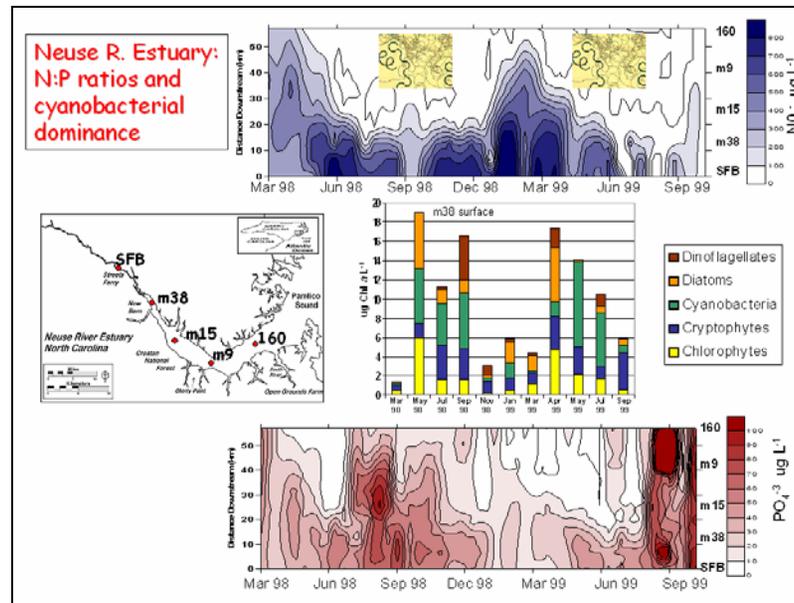


Fig. 5. Relationship, in space and time, of nitrate and phosphate concentrations, and relative dominance by cyanobacteria in the Neuse River Estuary, NC. Phytoplankton composition along a transect of 5 locations ranging from the upper oligohaline to lower mesohaline segments of the estuary was determined using high performance liquid chromatographic (HPLC) analysis of diagnostic (for major algal groups) photopigments (see Paerl et al. 2003). The period during which N_2 fixing cyanobacteria were present is indicated by the photomicrograph in the upper frame.

Some CHABs thrive under the relatively low light conditions caused by increased turbidity accompanying eutrophication. Members of the non-N₂ fixing filamentous genus *Oscillatoria* can form metalimnetic blooms in nutrient- (N and P) enriched lakes and reservoirs. Odor and taste producing *Oscillatoria* spp. and *Lyngbya* spp. can be particularly problematic in drinking water reservoirs, where their ability to adapt to low light conditions provides them a niche and allows them to coexist with surface-dwelling genera, including *Anabaena*, *Aphanizomenon*, and *Microcystis*. The toxic N₂ fixing, filamentous heterocystous species *Cylindrospermopsis raciborskii* appears to be taking similar advantage in nutrient enriched, eutrophying subtropical and tropical freshwater ecosystems. This low light adapted species, has, within a matter of a decade, invaded eutrophying inland waters of central Florida, USA by blooming as cloudlike masses throughout the water column (Chapman and Schelske 1997). Even though *C. raciborskii* is able to fix N₂ to meet its N requirements (under P sufficient conditions), this CHAB also effectively competes with eukayotes and other cyanobacteria for combined N when available (Padisak 1997). Furthermore, it is capable of intracellularly storing P as polyphosphate bodies. This cockroach-like CHAB appears to be able to effectively exploit altered nutrient cycling and optical conditions resulting from eutrophication in Florida, other US Southeastern and Midwest regions. Nutrient addition bioassays indicate that *both* N and P reductions are likely needed arrest the explosive growth and expansion of this CHAB (Fig. 6).

Because planktonic and benthic bloom assemblages may have complex nutritional requirements, efforts aimed at reducing CHAB dominance by manipulating N:P ratios have met with mixed results. P input constraints are often the most feasible and least costly approach in freshwater systems. In certain cases, P cutbacks can be highly effective on their own (without parallel N removal), because; 1) they may reduce total P availability enough to reduce growth of *all* bloom taxa, and 2) they may increase N:P ratios enough to provide eukaryotic algae a competitive advantage over cyanobacteria. There are noteworthy examples where exclusive P reductions have led to dramatic declines in cyanobacterial dominance and bloom control. These include Lake Washington, WA, USA, where reduction of sewage-based P inputs led to profound reversal of eutrophication (Edmondson and Lehman 1981), Lake Erie (Laurentian Great Lakes) (Likens 1972), and Himmerfjärden fjord, Sweden, where reduction of wastewater, agricultural and industrial P discharges caused a rapid decline in CHABs (Elmgren and Larsson 2002). P reduction efforts were helped by a phosphate detergent ban in the mid-1980's (Paerl et al. 2004). Similarly, reductions in wastewater and agricultural P inputs have led to decreased cyanoHAB bloom activities in large European and Asian lakes (e.g., Lakes

Constance and Lucerne, Germany–Switzerland; Lake Trummen, Sweden; Lago Maggiore, Italy; Lake Biwa, Japan). In other cases, parallel N and P reductions have been needed to reduce bloom potentials. In ecosystems where large amounts of previously–supplied and/or naturally–occurring P reside in the sediments, both N and P reductions are required to reduce the size and duration of blooms (Vollenweider and Kerekes 1982).

In contrast to P–limited inland waters, brackish estuarine and full salinity coastal waters tend to be N–limited (oligohaline regions of estuaries can be N and P co–limited) (Ryther and Dunstan 1971, Nixon 1986, 1995). N–enriched estuarine and coastal waters have experienced a recent upsurge in algal blooms (Paerl 1988, Hallegraeff 1993, Richardson 1997). Reducing N inputs has been recommended as a means of stemming coastal eutrophication (Vollenweider et al. 1992, Elmgren and Larsson 2002, Boesch et al. 2002). In the Neuse River Estuary, North Carolina, USA, deteriorating water quality has prompted calls for an N input “cap” and an overall 30% reduction in N loading (Paerl et al. 1995, 2004). However, changes in N loading alone may result in shifts in ratios of dissolved N to P supply rates in this and other N–sensitive estuaries (Paerl et al. 2004). Altered N:P inputs impact microalgal communities far beyond a simple reduction in productivity and biomass, including shifts in species composition and possible selection for low N:P adapted species (Smith 1983, Tilman and Kiesling 1984). In particular, the phytoplankton community could become dominated by N₂ fixing cyanobacteria that may circumvent N–limitation imposed by N reductions. This is of particular concern in shallow estuarine and coastal waters having rich (marine) repositories of P stored in the sediments that can be recycled to the water column during periods of hypoxia. Recently (summer 1997), we observed N₂–fixing *Anabaena* strains in mesohaline (5–15 psu) segments of the Neuse River Estuary (Piehler et al. 2002). In a parallel laboratory study (Moisander et al. 2000), two toxic Baltic Sea *Nodularia* strains and native *Anabaenopsis* and *Anabaena* species were capable of growth and proliferation in Neuse River Estuary water over a wide range of salinities, demonstrating the potential for CHAB expansion in estuaries (Fig. 7).

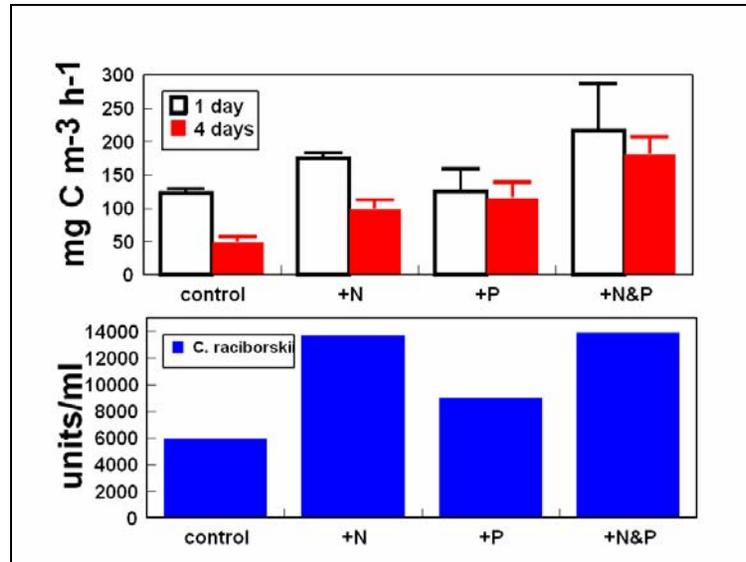


Fig. 6 Upper frame. Results from *in situ* nutrient addition bioassay, showing the effects of N (as 20 $\mu\text{M NO}_3^-$) and P (as 5 $\mu\text{M PO}_4^{3-}$), added singly or combined, on primary productivity of Lake George, a lake located in the upper St Johns River system, Florida. This lake has supported blooms of the invasive CHAB *Cylindrospermopsis raciborskii*. Lower frame shows the effects of these nutrient additions on *C. raciborskii* biomass as numbers of filaments or “units” per ml. These bioassay results indicate that growth of the entire phytoplankton community and *C. raciborskii* is stimulated by N and P additions individually and combined, support for a dual nutrient reduction strategy.

Both diazotrophic and non-diazotrophic CHABs can utilize diverse forms of combined N (inorganic and organic) (Paerl 1988). This nutritional flexibility may provide a key competitive advantage in response to anthropogenic N loading events. Large pulses of non-point source N loading have increased and are drivers of freshwater and marine eutrophication (Nixon 1995, Vitousek et al. 1997, Paerl 1997, 1998). Cyanobacterial growth and bloom responses in N-limited North Carolina estuaries closely track (in time and space) such events (Pinckney et al. 1997, 1998). In particular, organic N and ammonium-enriched conditions may favor cyanobacteria (Pinckney et al. 1997) and toxicity of bloom genera (Paerl and Millie 1996). Earlier observations of such correlations in nature (Pearsall 1932, Fogg 1969) have been largely overlooked, but might be relevant.

Non-N₂ fixing planktonic and benthic CHAB genera, including *Microcystis*, *Lyngbya*, and *Oscillatoria*, can also exploit these N loading scenarios. *Microcystis* blooms tend to be confined to oligohaline waters, while *Oscillatoria* and *Lyngbya* can thrive in seawater salinities. These genera thrive under relatively low N:P ratios, as long as adequate P supplies exist (Smith 1990, Paerl 1990). Estuaries with relatively abundant P supplies (natural or anthropogenic) and growing (non-point) N inputs are potential targets for these CHABs. In particular, systems susceptible to bottom water anoxia accompanied by sediment N and P release events may be vulnerable.

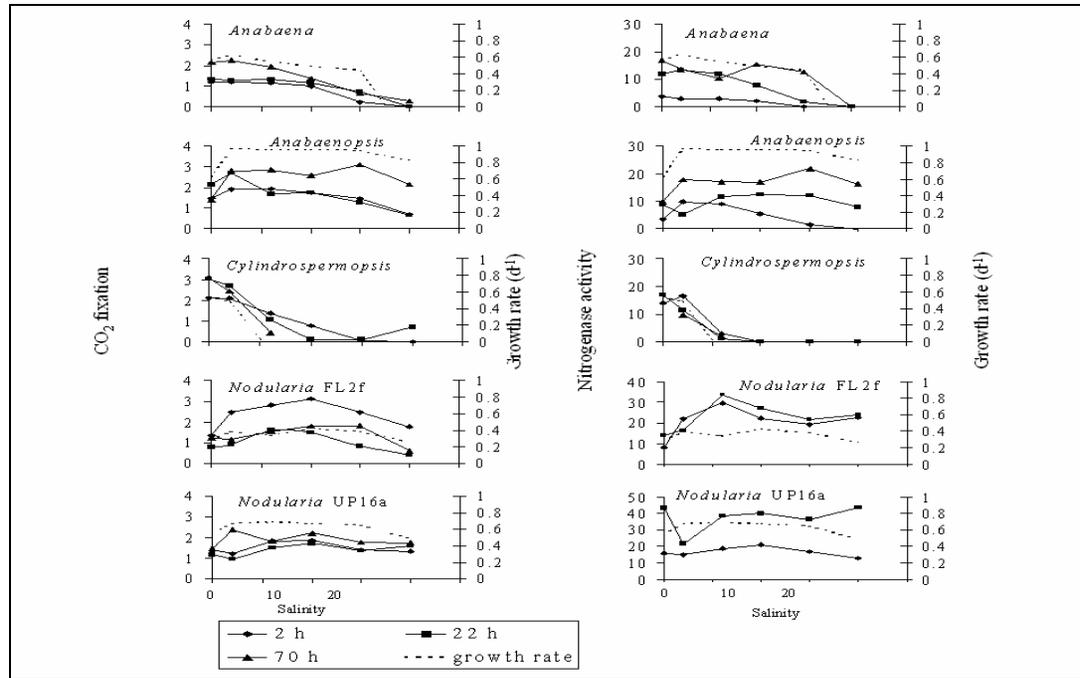


Fig. 7. Salinity effects on photosynthesis (CO₂ fixation), growth, and nitrogen fixation (nitrogenase activity) of some common N₂ fixing CHABS. Figure adapted from Moisander et al. (2002a)

Options for CHAB Control

As shown above, ecosystem level, physical, chemical and biotic regulatory variables often co-occur and may interact synergistically and antagonistically to control the activities (N_2 fixation, photosynthesis) and growth of CHABs (Paerl 1988, Paerl and Millie 1996). Thus, overriding, easily-executed controls are desirable.

Means of controlling blooms include; 1) applications of algacides, the most common of which is copper sulfate, 2) nutrient input reduction and manipulation (of N:P ratios), 3) disrupting vertical stratification, through either mechanically or hydrologically induced vertical mixing, 4) reducing retention time (increasing flushing) of bloom-impacted waters, and 5) biological manipulation. Option 1 has been used in small impoundments, such as ponds and small reservoirs. This approach is not advised in larger ecosystems, or any waters to be used for fishing, drinking water and other animal and human use purposes, unless the system is drained after algacide application, flushed several times and refilled with algacide-free water. If the bloom-affected water body is small and accessible enough for installing destratification equipment, option (3) may be feasible. If abundant water supplies (i.e., upstream reservoirs) are available for hydrodynamic manipulative purposes, option (4) may be possible. Biological manipulation (5) encompasses a number of approaches to change the aquatic food web to increase grazing pressure on cyanobacteria or to reduce recycling of nutrients. Biomanipulation approaches can include introducing fish and benthic filter feeders capable of consuming cyanobacteria, or introduction of lytic bacteria and viruses. However, the most common biomanipulation approaches are intended to increase the abundance of herbivorous zooplankton by removing zooplanktivorous fish or introducing piscivorous fish. Alternatively, removal of benthivorous fish can reduce resuspension of nutrients from the bottom sediments. Questions have been raised about the long-term efficacy of curtailing cyanobacterial blooms by increasing grazing pressure, because this may lead to dominance by ungrazable or toxic strains (McQueen 1990; Ghadouani et al. 2003). Presently, biomanipulation is viewed as one component of an integrated approach to water quality management in circumstances in which nutrient reductions alone are insufficient to restore water quality (Moss et al. 1996, Scheffer 1998, Elser 1999). Otherwise, option 2 is the most practical, economically feasible, environmentally-friendly, long-term option. Below we will consider P and N management options for mitigating CHABs.

Phosphorus

Phosphorus inputs to aquatic ecosystems are dominated by; 1) non point source surface runoff, and 2) point sources such as effluents from wastewater treatment plants, industrial and municipal discharges, and 3) subsurface drainage from septic systems and groundwater. Among these, point sources have been the focus of P reductions. In many watersheds, targeting point sources is attractive, as they can account for a highly significant share of P loading. Point sources are readily identifiable, accessible, and hence from a regulatory perspective, easiest to reduce and manage.

In agricultural and urban watersheds, non-point surface and subsurface P inputs are of increasing concern. Increased P fertilizer use, generation and discharge of animal waste, soil disturbance and erosion, conversion of forests and grasslands to row-crop and other intensive farming operations, and the proliferation of septic systems accompanying human population growth are rapidly increasing non-point P loading. In agricultural and urbanizing watersheds, non-point sources can account for at least 50% of annual P loading. Because of the diffuse nature of these loadings, they are more difficult to identify and address from a nutrient management perspective.

As with nitrogen, the manner in which P is discharged to P-sensitive waters pays a role in controlling CHABs. Considerations include; 1) total annual (i.e., chronic) P loading, 2) shorter-term seasonal and event-based pulse (i.e., acute) P loadings, 3) particulate vs. dissolved P loading, and 4) inorganic vs. organic P loading. With respect to ecosystem P budgets and long-term responses to P loadings (and reductions), annual P inputs are of fundamental importance. However, when considering CHAB dynamics, seasonal and shorter-term acute loading events are of critical, and at times, overriding importance. When and where P enrichment occurs can determine the difference between bloom-plagued vs. bloom-free conditions. For example, if a large spring P discharge event precedes a summer of dry, stagnant (stratified) conditions in a relatively long residence time water body, the spring P load will be available for summer bloom development and persistence. Effective exchange and cycling between the water column and bottom sediments can retard P transport and hence retain P. As a result, acute P inputs during high flow periods may be retained longer than estimated based on water flushing time alone. In effect, water bodies exhibit both rapid biological responses to and a “memory” for acute P loads.

Unlike N, P exists in relatively few dissolved and particulate forms in natural waters. No gaseous forms of P are common, although under anaerobic conditions, trace amounts of the unstable gas phosphine (PH_3) may be generated. Overall, the main concern is with dissolved vs. particulate

forms of inorganic and organic P. Dissolved inorganic P (DIP) exists as orthophosphate (PO_4^{3-}), which is readily assimilated by all CHAB taxa. Many CHABs can accumulate assimilated P intracellularly as polyphosphates. Polyphosphates can serve as internal stores of P, for subsequent use in the event of ambient P depletion (Healy 1982). Dissolved organic P (DOP) can be a significant fraction of the total dissolved P pool. DOP can be assimilated by bacteria, microalgae and cyanobacteria, although not as rapidly as PO_4^{3-} (Lean 1973). A large fraction of the assimilated DOP is microbially recycled to DIP, enhancing P availability. The role of particulate P (as inorganic or organic forms) in aquatic production and nutrient cycling dynamics is less well understood. Particulate P (PP) may provide a source of DIP and DOP via desorption and leaching, and it may serve as a sorption/precipitation site for DIP. PP therefore exists in dynamic equilibrium with the dissolved phases of P. It is safe to assume that some fraction of the PP can serve as a source of biologically–available P and hence play a role in CHAB dynamics. On the ecosystem–scale, sedimented PP serves as an important source of stored P for subsequent release, especially during hypoxic/anoxic periods. It is prudent to include *both* dissolved and particulate P when formulating and managing P inputs and N:P ratios.

Nitrogen

Nitrogen exists as dissolved, particulate and gaseous forms. Many of these forms are biologically–available and readily exchanged within and between the water column and sediments. In addition, biological nitrogen (N_2) fixation and denitrification control the exchange between inert gaseous atmospheric N_2 and biologically–available combined N forms. Combined forms of N include dissolved inorganic N (DIN; including ammonium (NH_4^+), nitrate (NO_3^-) and nitrite (NO_2^-)), dissolved organic N (DON; e.g., amino acids and peptides, urea, organo–nitrates), and particulate organic N (PON; polypeptides, proteins, organic detritus). These sources can be supplied as non–point and point sources. Non–point sources include surface runoff, atmospheric deposition and groundwater, while point sources are dominated by municipal, agricultural and industrial wastewater. In rural and agricultural settings, non–point N inputs tend to dominate (>50% of total N loading), while in urban centers, point sources often dominate. All sources contain diverse organic and inorganic N species in dissolved and particulate forms; representing a mixture of biologically–available DIN, DON and PON that plays a critical role in the eutrophication process. Depending on sources, chemical makeup, delivery mecha-

nisms and spatial distribution of N inputs, ecosystem response can vary dramatically.

N inputs are dynamic, reflecting land use, population and economic growth. The means and routes by which human N sources impact and mediate estuarine and coastal eutrophication are changing. Among the most rapidly-growing (amount and geographic scale) sources of human N loading are surface runoff, groundwater and atmospheric deposition. Atmospheric N loading is an often-overlooked, but expanding source of *new* N loading to N-sensitive waters. In eastern North Carolina, the combined emissions of fossil fuel combustion (NO_x) and volatilization of NH_3 from stored animal waste (lagoons and land-applied) are a major (>30% of *new* N loading), rapidly-growing source of biologically-available N. Surface and groundwater N releases from expanding animal operations and urbanization are of additional concern.

The contribution of groundwater and atmospheric N to coastal watershed and oceanic N budgets will increase substantially as we enter the next century, when nearly 70% of North American and European populations will reside within 50 km of the coast (Vitousek et al. 1997). Globally, it is estimated that AD-N accounts for $\sim 40 \text{ Tg N y}^{-1}$, compared to $\sim 30 \text{ Tg N y}^{-1}$ from riverine discharge, $\sim 10 \text{ Tg N y}^{-1}$ for groundwater and $\sim 20 \text{ Tg N y}^{-1}$ for biological nitrogen fixation (Paerl and Whitall 1999). A significant fraction of atmospheric N is directly deposited to N-sensitive estuarine and coastal waters, bypassing the estuarine N "filter". In many locations, including the US Eastern Seaboard, Europe, and East Asia atmospheric N is among the dominant sources of anthropogenic N to the coastal zone. When and where anthropogenic N inputs are intercepted are critical determinants of ecosystem sensitivity, water quality responses and resourcefulness in response to N enrichment. The ramifications of this previously "out of sight out of mind" but growing new N source in algal bloom, including CHAB, dynamics should be investigated.

There is increasing emphasis on reducing N inputs to control estuarine and coastal eutrophication (c.f. Boesch et al. 2001, Elmgren and Larsson 2002). While this is undoubtedly a step in the right direction, the ramifications of reducing N relative to P in coastal waters with regard to CHAB bloom potential needs to be carefully assessed. North Carolina's Neuse River Estuary has been the site of periodic massive blooms of the toxic, surface scum-formers *Microcystis aeruginosa* and *Oscillatoria* spp. Dominance by these non- N_2 fixers attests to the current N "overload situation" (Paerl 1987, NC DENR 1988). Dilution bioassays and historic N loading trend data indicate that watershed loading of N would need to be reduced by at least 30% to obtain N-limited conditions during the critical spring bloom initiation period (Paerl et al. 1995). Accordingly, a 30% N

reduction has been legislatively mandated (since 1997), and is the target of a Total Maximum Daily (N) Load (TMDL) imposed by the US EPA (NC DENR 2001).

A complicating aspect nitrogen reduction strategies in the Neuse River is the presence of N_2 fixing cyanobacteria, *Anabaena*, *Aphanizomenon*, and *Anabaenopsis*. This, combined with evidence that P loading also is excessive (Paerl 1987, Stow et al. 2001), suggests that if N loading is reduced by 30% without parallel P reductions, there may be potential for replacing non- N_2 fixing *Microcystis* with N_2 -fixing *Anabaena* or *Aphanizomenon* blooms (Piehler et al., 2002). Similarly, there is concern that reducing N without maintaining strict reductions on P inputs to control eutrophication in Sweden's Himmerfjärden, may allow CHABs to regain dominance (Elmgren and Larsson 2001). Indeed, initial reductions of N in this fjord draining to the Baltic Sea have led to an increase in cyanobacterial biomass (Elmgren and Larsson 2001). Detailed and timely monitoring of phytoplankton community trends as N reductions proceed to stem cultural eutrophication in these and other brackish water systems will enable managers to formulate N and P loadings aimed at de-eutrophication without promoting CHABs.

Conclusions

CHABs are globally distributed and regulated by an interplay of geographically- and ecologically-diverse environmental variables. The long evolutionary history of bloom taxa has led to both tolerance and adaptability to short-term (i.e., diel, seasonal, decadal) and longer-term (geological) environmental change, making these photosynthetic prokaryotes a “group for all seasons”.

In this contribution, I have explored the interactive physical, chemical and biotic factors implicated in the development, proliferation and expansion of CHABs. Despite their seemingly infinite adaptation to environmental change on both geological and biological time scales, cyanobacterial nuisance characteristics (e.g., large anoxia-generating and toxic blooms) are impacted by human alterations of aquatic environments. The most notable and controllable alterations include; 1) nutrient (especially N and P) enrichment, 2) hydrological changes, including freshwater diversions, the construction of impoundments such as reservoirs, water use for irrigation, drinking, flood control, all of which affect water residence time or flushing rates. In smaller waterbodies (<50 hectares) destratification of bloom-impacted waters by mechanically-induced vertical mixing or bub-

bling, and application of algacides such as copper salts and herbicides are options. Algacide applications are only feasible in small impoundments that are not to be used for consumption (either water, fish or shellfish) or recreational purposes (bathing). Furthermore, algacides need to be applied repeatedly, and thus unlike nutrient reductions, are not an effective long-term bloom reduction strategy. Biological controls, such as the introduction and manipulation of grazers (from zooplankton to fish), lytic bacteria, viral cyanophages, and antibiotics have been proposed as controls, but remain highly experimental and have not been broadly effective. Hence, they are not discussed in detail here.

Effective long term control and management of nuisance, particularly toxin-producing, CHABs should consider the interactive nature of above-mentioned physical, chemical and biotic factors known to play regulatory roles. In addition, knowledge of the ecological and physiological adaptations that certain taxa possess to circumvent specific environmental controls is of central importance. These include; 1) the ability of N_2 fixing taxa to exploit N-limited conditions, 2) the ability of certain buoyant taxa to counteract mixing and other means of man-induced destratification aimed at minimizing cyanobacterial dominance, 3) specific mutualistic and symbiotic associations that cyanobacteria have with other microorganisms, plants and animals, which may affect CHAB community structure and function.

Lastly, we should strive to better understand the potential roles toxins might play in bloom dynamics. Progress in identifying and understanding the roles toxins and other metabolites play in the physiology and ecology of bloom-forming cyanobacteria may be achieved by integrating physiological, toxicological and ecological perspectives and expertise. This includes hypothesis testing and problem solving using interdisciplinary experimental, monitoring and assessment approaches. In addition, the synthesis of well defined laboratory experimental work with ecosystem-level studies utilizing similar techniques and measurements will prove invaluable in unraveling the complexity of environmental regulation of cyanobacterial blooms. We are at the threshold of more holistic approaches to environmental problem solving. In this regard, the advent and incorporation of novel analytical and molecular identification and characterization techniques in environmental biology and management will prove invaluable and indispensable.

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