8 Ecology of Harmful Cyanobacteria

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8.1 Introduction

Cyanobacteria (blue-green algae) are the Earth's oldest known (>2.5 billion years) oxygenic phototrophs, yet today still exhibit remarkable adaptations and diversification in response to evolutionary change. This physiologically and ecologically diverse microbial group has survived and adapted to the range of geochemical changes marking the evolution of the Earth's biosphere. Recently, cyanobacteria have exploited human alterations of aquatic environments, most notably nutrient-enhanced primary production, or eutrophication (Fogg 1969). Worldwide, cyanobacterial blooms are visible, well-documented, widespread indicators of freshwater, brackish and marine eutrophication. Toxic blooms pose serious water quality, fisheries resource, animal, and human health problems (Chorus and Bartram 1999; Huisman and Visser 2005), including foul odors and tastes, hypoxia, and fish kills. Nutrient cycling and food web dynamics may be altered, and blooms can contribute large amounts of "new" C and N as fuel for hypoxia and anoxia (Horne 1977).

Harmful cyanobacterial blooms (CyanoHABs) have been present for centuries in eutrophic inland, estuarine, and coastal waters (Fogg 1969; Paerl 1988). Proliferation into more recently eutrophying waters is also underway. Examples include expansion of planktonic N_2-fixing and non-N_2-fixing genera (Table 8.1) in lacustrine, riverine, estuarine, and coastal habitats worldwide (Paerl et al. 2001). Aquaculture operations are also susceptible to cyanoHAB invasions. Molecular analyses indicate that the diversity of cyanoHABs at genera, species and strain levels is much greater than observed microscopically (Dyble et al. 2002) (Fig. 8.1). Using N_2-fixing gene (*nifH*) sequence analysis techniques, MacGregor et al. (2001) recently detected the notorious Baltic Sea N_2-fixing bloom former *Nodularia* spp. in oligo-mesotrophic Lake Michigan.

Benthic filamentous and coccoid genera (Table 8.1) can also undergo explosive growth in diverse habitats ranging in salinity. Blooms of the non-

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Table 8.1. Non-N_2-fixing and N_2-fixing filamentous non-heterocystous (*FNH*), coccoid (*C*), and heterocystous filamentous (*HF*) cyanoHAB genera

Genus	Habitat	Freshwater(F)/ Estuarine(E)/Marine(M)
Non-N_2-Fixing		
Microcystis (C)	Planktonic	F, E
Oscillatoria (FNH)	Planktonic/benthic	F, E, M
Planktothrix (FNH)	Planktonic	F, E
N_2-Fixing		
Anabaena (HF)	Planktonic/benthic	F, E, M
Aphanizomenon (HF)	Planktonic	F, E
Calothrix (HF)	Benthic	F, E, M
Cylindrospermopsis (HF)	Planktonic	F
Lyngbya (FNH)	Planktonic/benthic	F, E, M
Nodularia (HF)	Planktonic	F, E, M
Nostoc (HF)	Planktonic/benthic	F, E, M
Scytonema (HF)	Planktonic/benthic	F, E, M

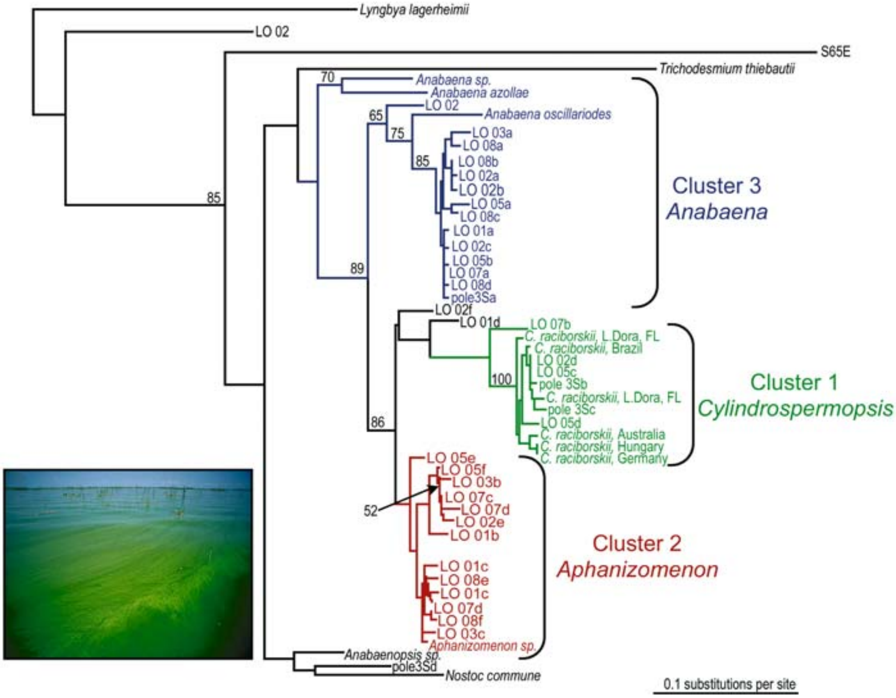

Fig. 8.1. Diversity of N_2 fixing cyanoHABs, based on sequence analysis of the N_2-fixing gene *nifH*, from Lake Okeechobee, Florida. Only six heterocystous cyanoHAB species were identified microscopically. Bootstrap values of >50 % are given next to the corresponding nodes. *Desulfovibrio gigas* (GenBank accession #u68183) was used as the outgroup. From Dyble et al. (2002)

heterocystous filamentous genera *Lyngbya* and *Oscillatoria* are becoming more numerous and persistent in nutrient-enriched springs, rivers, reservoirs, estuarine and coastal embayments, and reefs (Speziale and Dyck 1992; Lapointe 1997; Dennison et al. 1999). Benthic CyanoHABs are indicative of eutrophication and decreased grazing by herbivorous fishes due to overfishing. Their adverse impacts include smothering seagrass communities, corals and mudflats, negatively affecting infauna (Dennison et al. 1999; Paul et al. 2001). Some *Lyngbya* strains produce toxic secondary metabolites (Paul et al. 2001), including aplysiatoxins, debromoaplysiatoxin, and lyngbyatoxin A, metabolites of *L. majuscula*, causative agents of the acute dermal lesions following contact with this cyanoHAB. These compounds are protein kinase C activators and potent tumor promoters *in vivo*, issues of broad public health concern (Mynderse et al. 1977 cited in Paul et al. 2001). *Lyngbya* strains also fix N_2 (Jones 1990), which explains why P may stimulate growth more than N additions (Phlips et al. 1991). These strains thrive in N-deprived waters where N_2 fixation is advantageous, and they bloom in response to land-derived nutrients (N, P, Fe), and organic matter (Dennison et al. 1999).

8.2 Environmental Factors Controlling CyanoHABs

Interactive physical, chemical and biotic factors involved in the control of cyanoHAB growth and dominance are shown in Fig. 8.2.

8.2.1 Nutrients

Among the macronutrients required for aquatic plant growth, nitrogen (N) and phosphorus (P) are often in shortest supply relative to need. In most freshwater ecosystems, excessive P loading has been linked to eutrophication. P-driven eutrophication may favor the development of either N_2-fixing or non-N_2-fixing cyanobacteria, especially if the affected water body exhibits relatively long residence times (low rates of flushing), high surface water temperatures (>20 °C), and strong vertical stratification (Paerl 1988). N_2-fixing cyanobacterial dominance depends on several factors, most notably the availability of biologically utilizable nitrogen relative to phosphorus. Systems having low molar ratios of total and soluble N to P (<15) appear most susceptible to cyanobacterial dominance (Smith 1990). In some instances, the "N:P rule" does not apply. For example, Downing et al. (2001) showed that increased nutrient concentrations and loadings of N and P were better predictors of CyanoHAB dominance. Other exceptions include; (1) highly eutrophic systems in which *both* N and P inputs may exceed the assimilative capacity of the phytoplankton, and (2) well-flushed systems, in which the flushing rate

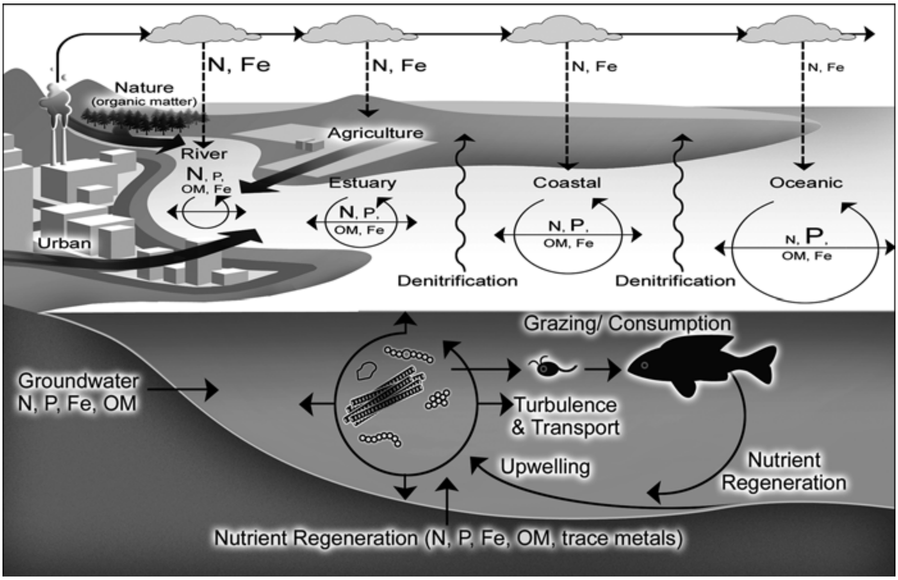

Fig. 8.2. Illustration of the interactive physical, chemical and biotic variables controlling CyanoHAB expansion across the freshwater–marine interface

exceeds the maximal cyanobacterial growth rates, typically >1 d^{-1}. In N- and P-enriched systems, N:P ratios may be >20, but since both N and P may be supplied in excess, factors other than nutrient availability (e.g., irradiance, vertical mixing, residence time, salinity, micronutrients) may dictate algal community dynamics. Here, N_2 fixation confers no advantage, and non-N_2-fixing taxa will predominate.

Moderately N- and P-enriched waters can support diazotrophic and non-diazotrophic species sequentially. During the wet spring months, non-point source runoff, which tends to be high in N, dominates. Later, during drier summer months external N loads decrease, and P-rich point source inputs and internal nutrient cycling dominate. Resultant relative P enrichment (i.e., declining N:P ratios) will select for N_2-fixing species (Paerl 1988). Once N_2 fixers are established, non-diazotrophic species may coexist, because they are able to utilize fixed N produced and released by N_2 fixing species (Paerl 1990). Co-occurring diazotrophic and N-requiring bloom species are capable of buoyancy regulation, and thus a near-surface existence, in turbid productive waters. Mixed assemblages can persist as bloom "consortia" throughout the summer and fall months (Paerl et al. 2001), until unfavorable physical conditions including rapid cooling (<15 °C) and turnover take place. Because these assemblages have complex nutritional requirements, efforts aimed at reducing cyanobacterial dominance by manipulating N:P ratios have met with mixed results.

P input constraints are often the preferred, least costly approach. In certain cases, P cutbacks can be effective on their own (without parallel N removal), because; (1) they may reduce total P availability enough to control growth of *all* bloom taxa, and (2) they may increase N:P ratios enough to provide eukaryotic algae with a competitive advantage over cyanobacteria. Examples include; Lakes Washington and Erie, USA, and the Baltic Sea embayments and fjords of Sweden, where cyanobacterial blooms have been controlled by both point and non-point source P reductions (Edmondson and Lehman 1981; Elmgren and Larsson 2001).

Nitrogen-limited (i.e., P-sufficient) estuarine and coastal waters have also experienced a recent upsurge in algal blooms. This has been attributed to increases in anthropogenic N loading (Paerl 1988). In the Neuse River Estuary, NC, USA, deteriorating water quality due to excessive N loading has led to an N input "cap" and an overall 30 % reduction in N loading (Paerl et al. 2004). Reductions in N loading lead to lower N:P ratios, potentially selecting for N_2-fixing cyanobacteria that could circumvent N-limitation imposed by N reductions. During the summer of 1997, Piehler et al. (2002) observed N_2-fixing *Anabaena* strains in mesohaline segments of this estuary. In a parallel laboratory study (Moisander et al. 2002a), two toxic Baltic Sea *Nodularia* strains and native *Anabaenopsis* and *Anabaena* thrived in Neuse River Estuary water over a range of salinities, demonstrating the potential for estuarine cyanoHAB expansion (Fig. 8.3).

While diazotrophs have an advantage of subsistence on atmospheric N_2, they also proliferate on combined inorganic and organic N sources. In Florida's St. Johns River system, growth of the invasive, toxic, heterocystous cyanoHAB *Cylindrospermopsis raciborskii* can be stimulated by nitrate and/or ammonium, for which it competes well with eukaryotic phytoplankton during runoff-rich springtime (Fig. 8.4). During the drier summer months when N is chronically limiting, it switches to N_2 fixation as its main N source. This nutritional flexibility provides *C raciborskii* a competitive advantage in response to seasonal N loading.

Iron (Fe) and trace metal micronutrients are essential for cyanobacterial growth. Iron is a cofactor of enzymes involved in photosynthesis, electron transport, energy transfer, N (NO_3^- and NO_2^-) assimilation and N_2 fixation. Iron limitation of cyanobacterial growth has been demonstrated in freshwater (Paerl 1990) and marine ecosystems (Paerl et al. 1994 in Paerl and Zehr 2000). In oceanic and coastal regions removed from terrigenous or atmospheric Fe inputs, diazotrophic growth may be mediated by Fe availability. Populations of the bloom-forming N_2-fixing cyanobacteria *Trichodesmium* exhibited Fe-limited CO_2 and N_2 fixation in the W. Atlantic Ocean off the North Carolina coast (Paerl and Zehr 2000).

Bloom-forming cyanobacteria produce potent siderophore (hydroxamate) chelators capable of sequestering iron at low ambient concentrations (Murphy et al. 1976 in Paerl 1990). This may provide a competitive advantage over

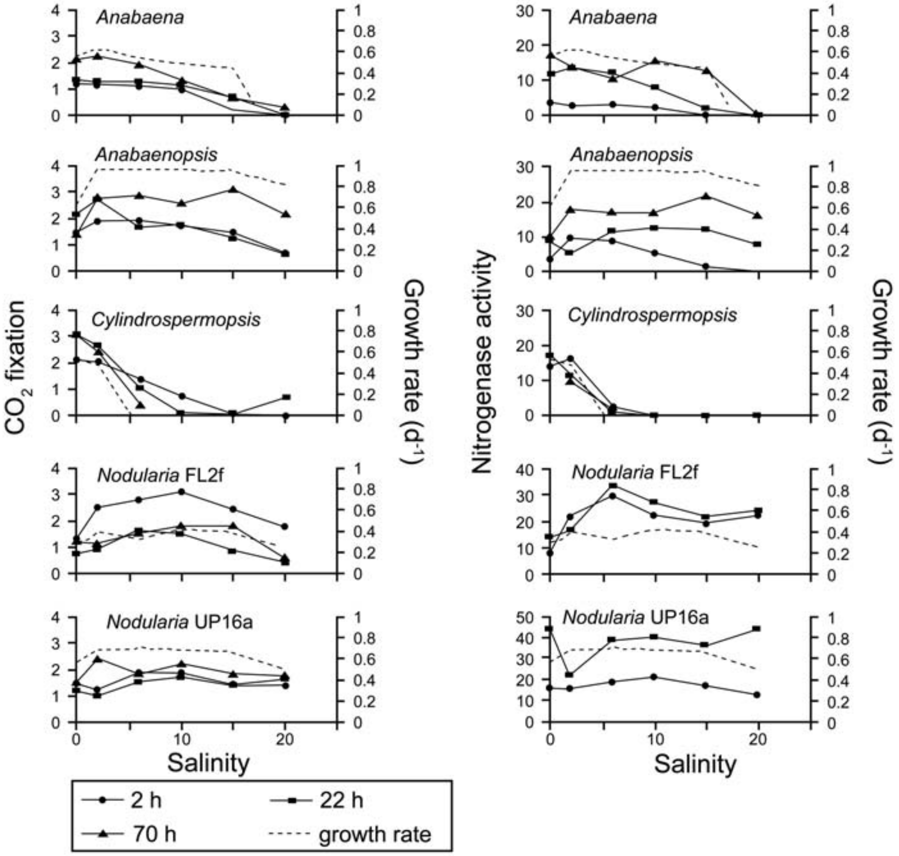

Fig. 8.3. Experimentally determined effects of salinity on CO_2 fixation (mgC mg Chl a^{-1} h^{-1}), nitrogenase activity (µmol C_2H_4 mg Chl a^{-1} h^{-1}), and growth of cyanoHABs found at the freshwater-marine interface. Salinity is in practical salinity units (PSU). Isolates of cyanoHABs used were obtained from the Baltic Sea, Neuse River Estuary (North Carolina), and lakes in Central Florida that drain into the St. Johns River and Estuary. Figure adapted from Moisander et al. (2002a)

eukaryotic phytoplankton when Fe availability is restricted. Bloom species may themselves affect Fe availability by mediating ecosystem productivity (i.e., organic matter production), bottom water hypoxia and anoxia, which can lead to the liberation of significant amounts of Fe, as soluble Fe^{2+}. Since most cyanoHABs are tolerant to sulfide that often accompanies hypoxia, these species are free to migrate into the Fe-rich hypolimnion to replenish Fe supplies.

Cyanobacteria require a suite of trace metals for metabolism, growth and reproduction. Manganese, cobalt, copper, molybdenum and zinc are most frequently mentioned. Photosynthesis and N_2 fixation require these metals for

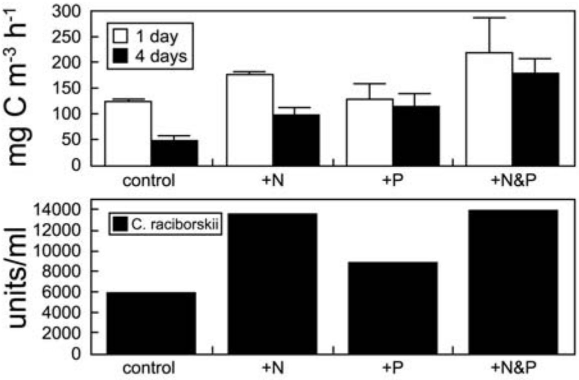

Fig. 8.4. Photosynthetic activity and growth response of Lake George, Florida, natural phytoplankton community to the additions of nitrogen (as nitrate at 20 mM N), phosphate (at 10 mM P) and N and P combined, in an in situ bioassay. Conducted during a period (May 2002) of dominance by the heterocystous cyanoHAB *Cylindrospermopsis raciborskii*. *C. raciborskii* accounted for approximately 70 % of cyanobacterial biomass and 40 % of total phytoplankton biomass during the bioassay period. Photosynthetic and growth responses were assessed after 24 and 72-h periods of nutrient enrichment, relative to untreated controls. Bioassays were conducted in 4-L transparent, polyethylene Cubitainers that were suspended in the water under natural irradiance and temperature conditions. Total phytoplankton community photosynthetic activity response was shown in the upper frame, while *C. raciborskii* response was specifically assessed using counts of filaments (normalized for length) shown in the lower frame. Results indicate that *C. raciborskii* growth was stimulated under individual N and P enrichment as well as combined N and P enrichment conditions, underscoring the broad competitive ability of the cyanoHAB to exploit nutrient enriched conditions

enzyme synthesis and function. Molybdenum (Mo) is a cofactor in the N_2-fixing enzyme nitrogenase. Howarth and Cole (1985 in Paerl and Zehr 2000) proposed that the relatively high (>20 mM) concentrations of sulfate (SO_4^{2-}), a structural analogue of the most common form of Mo found in seawater, molybdate (MoO_4^{2-}), could competitively (via the uptake process) inhibit N_2 fixation, thereby controlling this process. However, MoO_4^{2-} is highly soluble in seawater with concentrations in the order of ≈100 μM. Paulsen et al. (1991 in Paerl and Zehr 2000) showed that despite the potential for SO_4^{2-} competition, Mo was available at concentrations much lower than 100 μM. In W. Atlantic Ocean waters, N_2-fixing potentials were unaffected by this competition (Paulsen et al. 1991 in Paerl and Zehr 2000). It appears that cellular Mo requirements for N_2 fixation are met by sufficient uptake and storage. In addition, "alternative" non Mo-requiring nitrogenases exist in bacterial and cyanobacterial diazotrophs (Paerl and Zehr 2000). If such microbes are broadly distributed, they would have a mechanism circumventing Mo limitation.

Early studies (cf. Fogg 1969) cite dissolved organic matter (DOM) as a factor potentially controlling cyanobacterial blooms. The hypothesized mechanism for DOM-stimulated cyanobacterial growth is that DOM „conditions“ the water for cyanobacteria, possibly by inducing nutrient assimilatory enzymes and heterotrophy, or acting as nutrient (Fe and other trace metal) chelators, and providing a source of energy and nutrition for closely associated heterotrophic bacteria, which may form synergistic interactions with cyanobacteria (Paerl and Pinckney 1996). However, as pointed out by Fogg (1969), elevated DOM may be a result (due to DOM excretion, bacterial and viral lysis, and zooplankton „sloppy feeding“), rather than a cause of cyanobacterial blooms. Lastly, terrigenous organic substances discharged to coastal waters can regulate phytoplankton growth and composition. These substances interact with N and P availability to determine growth and dominance potentials of the N_2-fixing cyanoHAB *Nodularia spumigena* in the Baltic Sea (Panosso and Granéli 2000).

Cyanobacterial bloom taxa exhibit excellent CO_2 uptake kinetics, which are advantageous under dissolved inorganic carbon (DIC) limited conditions that can occur during blooms (Paerl 1988). This, combined with the ability to form buoyant surface blooms to obtain atmospheric CO_2 under DIC-limited conditions, provides a competitive advantage over eukaryotic algal taxa in nutrient-enriched, productive waters (Paerl 1988).

8.2.2 Physical-Chemical Factors: Salinity and Turbulence

Salinity, specifically ionic composition and strength, can inhibit growth among freshwater cyanoHABs (e.g., *Microcystis*, *Cylindrospermopsis*). However, salinity, per se, is not necessarily an across-the-board barrier to cyanobacterial growth and proliferation, as witnessed by the presence of diverse epiphytic and epibenthic N_2-fixing (e.g., *Calothrix, Lyngbya, Nostoc, Scytonema*) and non-N_2-fixing genera (e.g., *Oscillatoria*) in estuarine and coastal ecosystems (Potts 1994). Species of some benthic cyanoHAB genera, including *Lyngbya* and *Oscillatoria* are well adapted to freshwater or saline (including hypersaline) conditions. N_2- and CO_2-fixing activities in some freshwater cyanoHABs may be inhibited at increasing salt concentrations (Moisander et al. 2002a) (Fig. 8.3). Some indigenous populations can adapt to varying salinities by production of compatible osmolytes (Reed and Stewart 1985 in Paerl and Zehr 2000). Moisander and Paerl (2000) showed that Baltic Sea *Nodularia* were capable of diazotrophic growth under a wide range of salinities (0 to over 30 PSU).

8.2.3 Salinity and Turbulence

Turbulence over a range of scales (cellular to ecosystem) plays an important regulatory role in cyanoHAB bloom dynamics (Reynolds 1987; Kononen et al.

1996). CyanoHABs prefer calm, vertically stratified conditions, given adequate nutrient supplies (Paerl and Millie 1996). Following wind- or flow-induced destratification, cyanoHABs may lose their competitive advantage, and if such conditions persist, blooms can rapidly degrade or "crash". However, when intermittent weak stratification occurs during favorable growth periods (summer), cyanoHABs can quickly reemerge. Shallow, periodically mixed eutrophic lakes, the brackish Baltic Sea, reservoir and lagoonal ecosystems exhibit these tendencies. Ibelings et al. (1991) showed that periods of gentle intermittent mixing are preferred over consistently calm conditions, where colonial buoyant CyanoHABs like *Microcystis* can benefit from nutrient exchange during mixing, but then rapidly respond to an increase in water column stability by floating to the illuminated near-surface mixed layer.

Turbulence also affects phytoplankton growth rates and structural integrity. Among cyanobacteria, non-disruptive, low-level turbulence can promote localized „phycosphere“ nutrient cycling, alleviate certain forms of nutrient limitation (DIC, PO_4^{3-}, trace metals), and enhance growth. Gently stirred cultures of cyanoHABs frequently show higher growth than static cultures. Increases in turbulence either as stirring or shaking or more well-defined small-scale shear can, however, inhibit CO_2- and N_2-fixing activities and growth, with excessive turbulence causing disaggregation, cell and filament damage, and rapid death among diverse colonial genera in culture and in nature (Paerl 1990; Moisander et al. 2002b). Optimal CO_2, N_2 fixation and growth of these genera often rely on mutually beneficial microbial consortial interactions with host cyanobacteria. Turbulence can disrupt consortia and negatively affect growth (Paerl and Pinckney 1996).

Many bloom genera can regulate buoyancy by varying intracellular gas vesicles, a feature ensuring optimal (for growth) vertical orientation with respect to light and nutrient regimes in the water column (Reynolds 1987). In highly turbulent waters, the ability to maintain optimal vertical positioning can be overcome by mixing (Reynolds 1987), which may negatively affect growth and long-term competition for nutrient and radiant energy resources with eukaryotic phytoplankton. The turbulent conditions characterizing wind-exposed, well-mixed estuarine/coastal surface waters constrain N_2 and CO_2 fixation in CyanoHABs, and hence represent a potential barrier to their expansion (Paerl et al. 1995, in Paerl et al. 2001).

Despite their chronic N-limited condition and increasing nutrient loads, many estuarine and coastal waters do not show significant cyanobacterial dominance or blooms. Do physical constraints play a role in what appears to be an available niche for expansion from a nutrient perspective?

While non-N_2-fixing cyanoHAB taxa (e.g., *Microcystis* and *Oscillatoria* spp) are severely constrained in most N-limited, P-sufficient estuarine and coastal systems, diazotrophic taxa can, at times, proliferate in these waters; most often as endosymbionts in diatoms (*Rhizoselenia-Richelia*), or in benthic habitats. Adequate genetic diversity exists for potential colonization of diazotrophic cyanobacteria in estuaries (Paerl 2000; Paerl and Zehr 2000). Zooplankton and/or fish grazing do not appear to be the dominant mechanism explaining the scarcity of cyanobacteria in estuaries (Paerl et al. 2001). Turbulence has been proposed as a possible control in exposed, wind-mixed estuarine and coastal surface waters. This hypothesis has been tested in the laboratory using Couette chambers, capable of duplicating the shear rates experienced in a shallow wind-exposed (10–15 kt), N-limited estuary, the Neuse River Estuary, NC (Moisander et al. 2002b). These shear rates suppressed N_2 fixation and CO_2 fixation rates of *Anabaena* and *Nodularia* spp., relative to calm (low-shear) conditions. Persistent wind and shear in estuarine, coastal and oceanic waters may indeed be a constraint to cyanoHAB expansion.

8.3 CyanoHAB Interactions with Micro/Macroorganisms

CyanoHABs form close associations with other microorganisms in nature and in culture (Paerl and Kellar 1978 in Paerl 1990). Associated microorganisms include eubacteria, fungi, phytoflagellates, and protozoans (Paerl 1982 in Paerl 1990). These associations occur during all bloom phases, but the intensity and specificity of microbial epiphytism vary. During the initiation of *Anabaena oscillarioides* blooms, when high biomass-specific rates of CO_2 and N_2 fixation were observed, an association between the heterotrophic bacterium *Pseudomonas aeruginosa* and heterocysts prevailed (Gallucci and Paerl 1983 in Paerl 1990). The intensity and frequency of *P. aeruginosa* attachment to heterocysts exhibited a diel pattern, and *P. aeruginosa* was chemotactically attracted to *A. oscillarioides* heterocysts and N-containing compounds, including amino acids (Gallucci and Paerl 1983 in Paerl 1990).

Cyanobacteria excrete organic compounds, including organic and amino acids, peptides, alkaloids, carbohydrates and lipopolysaccharides. Excretion products both attract (chemotactically) and support the growth of phycosphere-associated bacteria (Paerl and Gallucci 1985). $^{15}N_2$ fixed by host *A. oscillarioides* was rapidly transferred to heterocyst-associated *P. aeruginosa* (Paerl 1984). Axenic isolates of *A. oscillarioides* showed optimal growth and N_2 fixation rates when inoculated with *P. aeruginosa* (Paerl and Kellar 1978), which specifically recolonized heterocysts.

Among *Oscillatoria* and *Lyngbya*, bacterized strains revealed higher growth rates and were easier to maintain in culture than axenic strains (Paerl 1982 in Paerl et al. 2001). Mutually beneficial mechanisms include exchange of nutrients, metabolites and gases as well as detoxifying roles of associated bacteria (Paerl 1986). Cyanobacterial toxins may mediate both antagonistic (protozoan and metazoan grazing, viral and bacterial lysis), and mutually beneficial consortial associations with heterotrophic bacteria (Paerl and Millie

1996). In this context, "toxins" are chemical mediators of microbial interactions and bloom dynamics.

Effects of cyanoHABs on higher trophic levels may occur through direct exposure to cyanotoxins, trophic transfer of toxins, or altered food chain structure (Paerl et al. 2001). CyanoHABs are often associated with decreases in abundance of large cladocerans and increases in importance of smaller cladocerans, rotifers and copepods (Leonard and Paerl 2005). Decreases in large cladocerans may be due to increased predation by planktivorous fish, or due to direct negative effects by cyanobacteria (Ghadouani et al. 2003). Inhibitory effects of cyanobacteria on grazing zooplankton may be due to interference with feeding as a result of awkward size or shape of filaments or colonies (Fulton and Paerl 1987 in Paerl et al. 2001; DeMott et al. 2001), chemical factors (toxicity, poor taste, poor nutritional value), or high abundances (i.e., blooms), which displace more nutritious non-bloom-forming algae or limit the ability of herbivores to utilize coexisting algae.

Cyanobacterial toxins can cause rapid mortality of herbivorous zooplankton (e.g., Fulton 1988; Rohrlack et al. 1999, both in Paerl et al. 2001), as well as long-term chronic effects on zooplankton growth and reproduction (e.g., Lürling 2003). While purified microcystin and anatoxin have toxic effects on zooplankton (Gilbert 1994 in Paerl et al. 2001), other compounds from cyanobacteria not generally considered to be "toxins" may be more inhibitory to zooplankton than known toxins (Rohrlack et al. 1999 in Paerl et al. 2001; Lürling 2003). Generally, toxic effects of "healthy" cyanobacteria on zooplankton appear to be due to consumption of cells containing endotoxins (Paerl et al. 2001; Rohrlack et al. 2001). However, filtrates or purified toxins from cyanobacteria can also inhibit herbivorous zooplankton (Paerl et al. 2001). Release of endotoxins from cyanobacteria during senescence or following treatment of blooms by algicides could have a strong impact on zooplankton communities.

Even when there is no evidence of cyanobacterial toxicity, unpalatability (Rohrlack et al. 1999 in Paerl et al. 2001) and poor nutritional value can adversely affect herbivorous zooplankton. Factors contributing to poor nutritional value include indigestibility and deficiency of highly unsaturated fatty acids (Ferrão-Filho et al. 2000). Although cyanobacteria are usually poor sole food sources for zooplankton, they can complement other food sources in mixed diets (Koski et al. 2002), suggesting that non-toxic cyanobacteria can contribute to zooplankton nutrition even when they do not dominate the phytoplankton community.

Microcystis aeruginosa can inhibit grazing rates, be poorly digested, or of poor nutritional value for herbivorous fish (Kamjunke et al. 2002). Fish kills associated with cyanobacterial blooms often result from oxygen depletion, but cyanobacterial toxins can also kill fish directly (Rodger et al. 1994 in Paerl et al. 2001). Conflicting evidence exists regarding effects of *Microcystis* on feeding rates and food selection by the zebra mussel, *Dreissena* (Vanderploeg et al. 2001; Pires et al. 2005). Cyanotoxins can accumulate in consumers, including freshwater clams, crayfish, zooplankton, gastropods, and fish (Paerl et al. 2001; Ibelings et al. 2005).

Although cyanobacterial blooms produce large biomass, their toxic and other inhibitory effects on grazers could produce alterations in aquatic food web structure that would reduce productivity of higher trophic levels. A shift in zooplankton composition from large cladocerans to smaller or more evasive cladocerans, rotifers and copepods may reduce the feeding success of young-of-the-year and other planktivorous fish. If cyanobacterial blooms exclude more nutritious algae, even zooplankton relatively resistant to cyanobacterial toxins may decrease in abundance and this could potentially lead to fish recruitment failures. Senescence or herbicidal treatment of blooms may release dissolved toxins, affecting organisms that would not normally consume cyanobacteria. Much of the biomass from these blooms probably enters microbial or detrital trophic pathways, with additional steps in the food chain reducing the potential productivity of fish and other commercially important species.

8.4 CyanoHAB Management

Ecosystem level, physical, chemical and biotic regulatory variables often co-occur and may interact synergistically and antagonistically to control N_2 fixation, photosynthesis and growth potentials of cyanoHABs (Paerl and Millie 1996) (Fig. 8.2). Potentially effective, achievable means of controlling bloom expansion include; (1) applications of algacides, the most common of which is copper sulfate, (2) nutrient input reductions and ratio manipulation, (3) disrupting vertical stratification, through 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 with considerable short-term success in small impoundments, including ponds and small reservoirs. This approach is not advised for larger ecosystems or any waters to be used for fishing, drinking water and other animal or human purposes. Likewise, in small water bodies, 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 includes approaches to increase grazing pressure on cyanoHABs and reduce recycling of nutrients. Biomanipulation approaches include introducing benthic filter feeders or fish (e.g., *Tilapia*) capable of directly consuming cyanobacteria from the water column, or introduction of lytic bacteria and viruses. 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

(Ghadouani et al. 2003). Presently, biomanipulation is viewed as one component of an integrated approach to water quality management when nutrient reductions alone are insufficient to restore water quality (Elser 1999). Overall, nutrient input controls remain the most effective and feasible long-term option.

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