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## Causes of Harmful Algal Blooms

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### 1.1 Introduction

Much has been written about the underlying causes of harmful algal blooms (HAB), the complex interplay of factors that lead to their proliferation, and the unique set(s) of factors contributing to blooms of different species of algae. In general, the overarching causes that have received much attention in the literature include degradation of water quality and increasing eutrophication; increasing aquaculture operations; transport of harmful species via ballast water or shellfish seeding, leading to new introductions; and climate change (e.g., Hallegraeff and Bolch, 1992; Hallegraeff, 1993; Anderson *et al.*, 2002; Glibert *et al.*, 2005, 2014a; Heisler *et al.*, 2008; Wells *et al.*, 2016; and references therein). This chapter reviews these complexities while highlighting the key role of changes in nutrients; estuarine/marine microalgal species are emphasized, and information is also included on some freshwater HAB. While some have suggested that increased monitoring or surveillance has led to a perception of an increase in HAB, there is now compelling evidence from many regions showing conclusively that increases in HAB proliferations are real, not sampling artifacts (Heisler *et al.*, 2008).

What is a HAB? In his seminal paper, Smayda (1997a, p. 1135) stated, “What constitutes a bloom . . . has regional, seasonal, and species-specific aspects; it is not simply a biomass issue. . . . The salient criterion to use in defining whether a ‘harmful’ species is in bloom and the distinctive feature of such blooms lie not in the level of abundance, but whether its occurrence has harmful

consequences.” Since the publication of that paper, biomass criteria for a few HAB species have been defined, but more generally HAB continue to be defined in terms of the extent to which they cause harmful events (fish kills), toxic events (shellfish and finfish poisoning), ecosystem disruption (nutritional and/or prey-size mismatches, such as picocyanobacterial blooms), or large biomass events (hypoxia or anoxia). In all cases, for a HAB to occur, the HAB species must be present and its biomass relative to other species in the assemblage changes, although the HAB species does not need to be dominant or in high abundance to elicit some of these effects.

In general, the factors that promote HAB can be reduced to two: changes in the rate of introductions of species to new areas and changes in local conditions leading to conditions more conducive to the growth of individual species. Environmental changes can be subtle and not all factors may change together, leading in some cases to situations where one factor may seem to be favorable, but growth is impaired due to a change in another factor. The success of an introduced species in a new environment is not ensured; instead, there must be a match of environmental factors and the species capable of exploiting the environment. As Smayda (2002) also wrote,

Anthropogenic seedings are not, in themselves, bloom stimulation events; they are only the first phase of a multi-phase process. A newly vectored, non-indigenous species is initially pioneering; it must either find an open niche or displace a niche occupant as its first step

towards successful accommodation within the community. . . . Until colonization is achieved, alien species introduced into water masses that have been modified by cultural nutrient enrichment, water mass conditioning by aquaculture, or climatological disturbances, will not bloom. Successful colonization alone is not decisive, it usually must be accompanied at some point, or coincide with habitat disturbance – a precondition for many HAB occurrences. (p. 292)

Changes in environmental conditions supportive of the increasing global occurrence of HAB are predominantly anthropogenic in nature, such as changes in nutrient loads resulting from expanding human population and associated nutrient pollution from agriculture and animal operations, alterations due to human changes in fishing pressure or aquaculture development, and/or large-scale changes in flow from major water diversion projects. However, changes in environmental conditions may also be due to interactions between trophic and biogeochemical changes that occur once new species become established, or to altered abiotic parameters or physical dynamics, such as temperature and stratification that are caused by climatic changes (e.g., Sunda *et al.*, 2006; Glibert *et al.*, 2011; Glibert, 2015; Wells *et al.*, 2016). The complex set of adaptive strategies associated with different species will lead to some species being more or less successful in contrasting environmental conditions (e.g., Margalef, 1978; Collos, 1986; Glibert and Burkholder, 2011; Glibert, 2015, 2016). The growth of some species can alter the biological and biogeochemical environment, in some cases changing the environment favorably for their own further growth, or for growth of other harmful species. No amount of pressure from an altered rate of species introductions will ensure success of that species in a new environment unless conditions are suitable for its growth (e.g., Smayda, 2002; Glibert, 2015). The success of HAB lies at the intersection of the physiological adaptations of the harmful algal species and/or strain (population), the environmental conditions, interaction with co-occurring organisms (both biogeochemically and trophodynamically), and physical dynamics that alter abiotic conditions and/or aggregate or disperse cells (or can alter abiotic conditions in a favorable or unfavorable manner), in turn promoting or inhibiting their growth. “Strain” is mentioned here because it is well established that there can be high intraspecific variation (strain differences) within a given harmful algal species in a wide array of traits ranging

from morphology, reproductive characteristics, and nutritional preferences to toxicity (Burkholder *et al.*, 2005; Burkholder and Glibert 2006, and references therein).

As stated by Wells *et al.* (2016, p. 69) in their review of HAB and climate change, for HAB to be successful, it depends on the “species ‘getting there’ . . . ‘being there’ as indigenous species . . . and ‘staying there.’” The same is true for nutrients and related environmental conditions. They must “get there,” often from anthropogenic sources; they must “be there”; and they must “stay there,” often through physical dynamics, changes in trophodynamics and biogeochemical processing, or climate-induced changes. Here, using the framework of getting there, being there, and staying there for both cells and nutrients and associated environmental factors, the complexity of factors influencing HAB, emphasizing the intersection of changing habitat, especially nutrient conditions, and adaptive capability of HAB are described. This chapter focuses mainly on microalgae, but also includes several examples of macroalgae. The chapter closes with some suggestions for advancement in the understanding of HAB and nutrients.

## 1.2 “Getting There”: The Classic Perspective on Introduced Species and Links to Cultural Eutrophication

### 1.2.1 Introduced Species

Transfers of species and their introductions to new areas occur frequently through various pathways. Of particular concern are ballast water introductions (e.g., Hallegraeff, 2010, and references therein; see also Chapter 13, this volume). Many harmful algal species appear to be able to maintain viability during ballast water transport, so the inoculum in the discharge area is often viable (e.g., Burkholder *et al.*, 2007a). Ballast water exchange practices have been linked to the proliferation of previously rare or undetected harmful algae in discharge locations, such as certain toxigenic dinoflagellates in Australian waters (Hallegraeff and Bolch, 1992; Hallegraeff, 1998). Ballast water discharge can alter the abundances of harmful species and set up conditions where previously rare populations proliferate (e.g., Rigby and Hallegraeff, 1996; Forbes and Hallegraeff, 1998; Hallegraeff, 1998). While only a small percentage

of introduced species have become invasive and have caused significant detrimental impact in the receiving environment (Ruiz *et al.*, 1997), in estuaries where the problem has begun to be well studied, it has generally been difficult to separate, with certainty, native from non-native taxa (Ruiz *et al.*, 1997). The fact that many microbial species presently have widespread distributions may reflect a long history of global transport by ships, migratory waterfowl and other animals, winds, water currents, and other mechanisms (Burkholder *et al.*, 2007a, and references therein). The continuing effects of human activities in non-indigenous species introductions and the resulting economic and ecological impacts can be so major that entire ecosystems have been completely changed (Cohen and Carlton, 1995, 1998; Ruiz *et al.*, 1997, 1999).

The expansion of aquaculture worldwide has created another mechanism whereby species can be transported and introduced to new areas (Hégaret *et al.*, 2008 and references therein). Aquaculture products are often shipped worldwide, and harmful species can be carried with these products. Similarly, seed stock and feed are also shipped worldwide, creating opportunities for HAB “hitchhikers.” As will be developed in this review, once harmful algal species are introduced, many site-specific factors acting in concert – such as the available suite of nutrient supplies, climatic conditions, season, light regime, the presence of potential predators, mixing characteristics and other physical dynamics, and the presence/abundance of potential competitor microbiota – will control whether a given harmful species can successfully establish and thrive in the new area (e.g., Smith *et al.*, 1999).

### 1.2.2 Anthropogenically Introduced Nutrients

Over-enrichment of coastal waters by nutrients is a major pollution problem worldwide as the result of human population growth and the production of food (agriculture, animal operations, and aquaculture) and energy (Howarth *et al.*, 2002; Howarth, 2008; Doney, 2010). Population growth and increased food production result in major changes to the landscape, in turn increasing sewage discharges and run-off from farmed and populated lands. A major increase in use of chemical nitrogenous fertilizers began in the 1950s and is projected to continue to escalate in the coming decades (e.g., Smil, 2001; Glibert *et al.*, 2006,

2014a). The global manufacture of nitrogen (N)-based fertilizers has, in fact, increased from < 10 million metric tonnes N per yr in 1950 to >150 million metric tonnes per yr in 2013, with 85% of all chemical fertilizers having been produced since 1985 (Howarth, 2008; Glibert *et al.*, 2014a, and references therein). In contrast to the enormous expansion in the global use of chemical N fertilizers, use of phosphorus (P) fertilizers has shown a much smaller increase, at a rate only about a third that of N (Sutton *et al.*, 2013; Glibert *et al.*, 2014a). Unlike N, there is no anthropogenic synthesis of P, and all P fertilizer comes from mined sources. Of these two major agricultural nutrients, only 10–30% actually reaches human consumers (Galloway *et al.*, 2002; Houlton *et al.*, 2013), and more than half is lost to the environment in direct run-off and atmospheric volatilization/eventual deposition (Galloway *et al.*, 2014).

Nearly 60% of all N fertilizer now used throughout most of the world is in the form of urea (CO [NH<sub>2</sub>]<sub>2</sub>) (Constant and Sheldrick, 1992; Glibert *et al.*, 2006; IFA, 2014). World use of urea as a fertilizer and feed additive has increased more than 100-fold in the past four decades (Glibert *et al.*, 2006). It is projected that from 2012 to 2017, an estimated 55 new urea manufacturing plants will be constructed worldwide, half of them in China (Heffer and Prud’homme, 2013), contributing to a further doubling of global urea use by 2050 (Glibert *et al.*, 2006, 2014a). Urea can be a significant contributor both to total N and to the fraction used by phytoplankton in estuarine and coastal waters (McCarthy, 1972; Harvey and Caperon, 1976; McCarthy *et al.*, 1977; Furnas, 1983; Kaufman *et al.*, 1983; Harrison *et al.*, 1985; Glibert *et al.*, 1991; Kudela and Cochlan, 2000; Switzer, 2008), and the frequency of reports that urea may be used preferentially by many harmful species has increased in recent years (Glibert *et al.*, 2006, and references therein). Urea also rapidly hydrolyzes to NH<sub>4</sub><sup>+</sup> in water, another important N form used by phytoplankton including HAB.

The development of concentrated (confined) animal feed operations (CAFOs) near coastal waters as well as inland is another increasing, major source of nutrient pollution (Mallin, 2000; Burkholder *et al.*, 2007b; United States Environmental Protection Agency, 2013). Animal agriculture is expanding to meet the dietary demands of an increasing population, and increasingly animal production is concentrated in large industrial feeding operations which results in dense animal populations per unit landscape area (Burkholder *et al.* 1997 and references therein). The high

concentration of wastes per unit area, in comparison to traditional animal production practices, commonly causes contamination of adjacent waters with nutrients and associated pollutants such as suspended solids and pathogenic microorganisms (Burkholder *et al.*, 2007b). To understand the scale of this nutrient source, as an example, in the Cape Fear River basin of North Carolina, it is estimated that there are 5 million hogs, 16 million turkeys, and 300 million chickens produced annually, yielding 82,700 tonnes of N and 26,000 tonnes of P in animal waste (Mallin *et al.*, 2015, and references therein). The estimated “manure footprint” for the United States is about 150,000,000 tonnes (Rumpler, 2016). In China, tens of thousands of CAFOs are estimated to produce more than 40 times as much N pollution as from other types of industries (Ellis, 2008).

Aquaculture can be an important nutrient source and, depending on the size of the operation and concentrations of animals, can be regarded as an aquatic form of CAFO. Nutrient inputs from large-scale culture of finfish, shellfish, macroinvertebrates, and even macroalgae in some areas (Wang *et al.*, 2015) are a growing concern as the importance of aquaculture in providing food supplies continues to escalate. From 1980 to 2012, world aquaculture production volume increased at an average rate of 8.6% per year, and world food fish aquaculture production more than doubled, from 32.4 million metric tonnes to 66.6 million metric tonnes (FAO, 2014). China, in particular, has sustained what has been described as a “dramatic expansion” in cultured fish production; in 2013 alone, it produced 43.5 million tonnes of food fish and 13.5 million tonnes of algae, or about two-thirds of the cultured fish and more than half of the cultured algae worldwide (FAO, 2014).

Localized impacts of “high-input/high-output” finfish and crustacean aquaculture can be severe, such as hypoxia and anoxia, nutrient over-enrichment from discharged waste food and excretory materials, and a shift in sediment biogeochemical processes and benthic communities below fish pens (Carroll *et al.*, 2003; Bissett *et al.*, 2006; Buschmann *et al.*, 2006; Kawahara *et al.*, 2009; Burridge *et al.*, 2010; Keeley *et al.*, 2014). Extreme water quality and habitat degradation have been documented in and around shrimp farms, in particular (Naylor *et al.*, 1998; Páez-Osuna, 2001, and references therein). The cultured species generally has a nutrient retention of 30% or less, the remainder being excreted to the enrichment or lost as undigested feed (e.g., Bouwman *et al.*, 2013a). Global cultured production of finfish and

crustacea contributed an estimated 1.7 million tonnes of N and 0.46 million tonnes of P to receiving waters during 2008 (Verdegem, 2013). Within the relatively short period from 2000 to 2006, nutrient release from shellfish cultures increased by 2.5- to 3-fold, and much larger increases are predicted in nutrient contributions from shellfish cultures by 2050 (Bouwman *et al.*, 2011). Aquaculture in many Asian countries is expanding at an apparently unsustainable pace. Asian aquaculture, mostly in China, now contributes nearly 90% of the total global marine aquaculture annually. During 2000–2010, nutrient release from all forms of mariculture in China collectively increased by 44% to 0.20 million tonnes of N, while estimated annual coastal N input from rivers increased by 10% to 2.7 million tonnes of N (Bouwman *et al.*, 2013b). Similar increases were estimated for P. By 2010, Chinese mariculture contributed about 7% of total N and 11% of total P inputs to coastal seas overall, and 4% and 9% of the dissolved N and P, respectively. Various HAB have been associated with estuarine/marine aquaculture, including toxic and fish-killing algae (Wu *et al.*, 1994; Honkanen and Helminen, 2000; Wang *et al.*, 2008; Furuya *et al.*, 2010), and high-biomass HAB (including macroalgae) are often linked to pond production (Alonso-Rodríguez and Páez-Osuna, 2003; Azanza *et al.*, 2005; Wang *et al.*, 2008).

Bivalve culture is generally considered to be less adverse and, in low densities, even benign (Burkholder and Shumway, 2011, and references therein). Nevertheless, when this type of aquaculture becomes so intensive that it exceeds the ecosystem carrying capacity, significant increases in nutrient supplies (especially  $\text{NH}_4^+$ ), noxious phytoplankton blooms, oxygen deficits, and symptoms of cultural eutrophication develop and indeed have been documented in poorly flushed lagoons and embayments (Burkholder and Shumway, 2011). A recent study in Chesapeake Bay, for example, showed an increase of 78% in total  $\text{NH}_4^+$  downstream from an oyster aquaculture facility (Ray *et al.*, 2015). Nutrient pollution from finfish and crustacean aquaculture generally is much higher than from molluscan culture, but, as Bouwman *et al.* (2013a) commented, because of relatively “low assimilation efficiency, molluscs can act as pumps in coastal seas transforming the nutrients in algal biomass to dissolved and particulate detrital nutrients; finfish and crustacea similarly act as pumps but with exogenous feed.”

In many regions, atmospheric deposition of N contributes significant pollution (e.g., Howarth,

2006; Duce *et al.*, 2008; Galloway *et al.*, 2008). This N is derived because of increasing NO<sub>x</sub> emission from fossil fuel burning and from volatilization of animal manures and other land-based fertilizer applications. In both European and U.S. coastal waters, anthropogenic atmospheric N deposition contributes from 10 to 40% of new N loading (Jaworski *et al.*, 1997). It has been estimated that N atmospheric deposition reaches >700 mg N m<sup>2</sup> per yr in many regions, particularly the downwind plumes from major cities (e.g., Duce *et al.*, 2008). In eastern North Carolina, atmospheric N deposition (NO<sub>x</sub>) has more than doubled since the 1970s, a result of urbanization, increased animal operations, and agricultural expansion (Mallin, 2000). Where animal manures dominate, such as in eastern North Carolina (Rothenberger *et al.*, 2009), NH<sub>4</sub><sup>+</sup> emissions account for half of all N deposition (Aneja *et al.*, 2003; Whitall *et al.*, 2003), which has implications for HAB as shown further in this chapter.

Overall, there are many sources of species introductions and diverse routes by which nutrients are contributed to the aquatic environment, across the salinity gradient. That is, there clearly are many paths for both harmful algal cells and nutrients to “get there.”

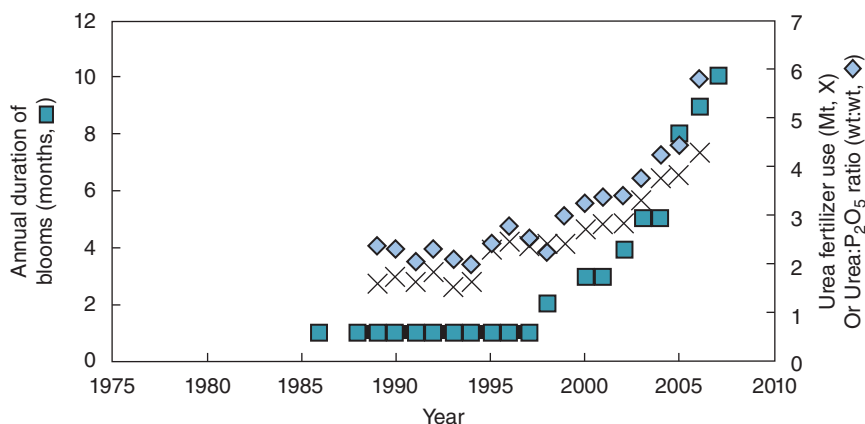
## 1.3 “Being There”: Blooms and Why They Succeed

### 1.3.1 Nutrient-Related HAB

Increased loading of both N and P has been strongly, positively related to human population density (Caraco, 1995; Smil, 2001). Well-documented examples illustrate an increase of some HAB in relation to increases in N and/or P loading (Lancelot *et al.*, 1987; Anderson *et al.*, 2002; Glibert and Burkholder, 2006; Vahtera *et al.*, 2007; Glibert, 2014a). Among high-biomass bloom formers, pelagic *Prorocentrum* species, especially *Prorocentrum minimum*, has been expanding in global distribution in concert with eutrophication, and in particular with N enrichment (Heil *et al.*, 2005; Glibert *et al.*, 2008, 2012). *Prorocentrum* sp. has been found to be common near sewage outfalls and also near nutrient-rich shrimp ponds (Cannon, 1990; Sierra-Beltrán *et al.*, 2005). In the Baltic Sea, its expansion has been linked to impacts from human activities (Olenina *et al.*, 2010). Worldwide, various species of harmful cyanobacteria have been stimulated to bloom in

over-enriched fresh and tidal fresh waters (Burkholder and Glibert, 2013, and references therein), and even in some brackish systems (e.g., McComb and Humphries, 1992; Vahtera *et al.*, 2007; McCulley, 2014). In Northern European waters, blooms of the mucus-forming HAB species *Phaeocystis globosa* have been directly related to the excess NO<sub>3</sub><sup>-</sup> content in riverine and coastal waters, that is, the NO<sub>3</sub><sup>-</sup> remaining after other species of algae deplete other nutrients (Lancelot *et al.*, 1987; Lancelot, 1995). In the United States, a strong positive relationship has been documented between increased NO<sub>3</sub><sup>-</sup> loading from the Mississippi River to the Louisiana shelf and increased abundance of the toxigenic diatom *Pseudo-nitzschia pseudodelicatissima*, based on the geological record of the siliceous cell walls of this species found in sediment cores (Parsons *et al.*, 2002). In Puget Sound, Washington, United States, a striking positive correlation has been found between the growth in documented cases of paralytic shellfish toxins over four decades and the growth in human population, based on United States Census statistics, strongly suggestive of nutrient loading and eutrophication as the causative agent of change (Trainer *et al.*, 2003).

Dinoflagellate blooms off the coast of China have expanded in geographic extent (from km<sup>2</sup> to tens of km<sup>2</sup>), duration (days to months), numbers of species, and harmful impacts, and these trends have paralleled an increase in N fertilizer use during the past several decades (Heisler *et al.*, 2008; Li *et al.*, 2009; Glibert *et al.*, 2011, 2014a). Annual N fertilizer use in China has escalated from about ~0.5 million tonnes in the early 1960s to 42 million tonnes around 2010, with the fraction of urea increasing nearly fivefold over just the past two decades (Glibert *et al.*, 2014a, and references therein). River export of N increased from 1980 to 2010 from ~0.5 to >1.2 tonnes km<sup>-2</sup> per yr in the Changjiang River, from ~0.1 to ~0.2 tonnes per km<sup>2</sup> per yr in the Yellow River, and from ~0.4 to >1.2 tonnes per km<sup>2</sup> per yr in the Pearl River basins (Ti and Yan, 2013). In parallel with these trends in nutrient loading, the number of HAB has increased in virtually all waters of China over the past three decades. In addition to these blooms, “green tides” have increased. These noxious macroalgal blooms (*Ulva prolifera*) received notoriety at the Qingdao Sailing Center during the 2008 Summer Olympics, when the water was blanketed with thick green scum (Hu *et al.*, 2010; Liu and Zhou, 2017). More recently, “brown tides” have become recurrent in the Yellow Sea (Zhang *et al.*, 2012).



**Figure 1.1** Change in annual duration of *Microcystis* blooms in Lake Tai (Taihu) in months, urea fertilizer use (million metric tonnes) scaled to that in the Changjiang watershed and the ratio of use of urea:P<sub>2</sub>O<sub>5</sub> fertilizer. *Source:* *Microcystis* data are from Duan *et al.* (2009), reprinted with permission of the American Chemical Society. Data sources for fertilizer use are given in Glibert *et al.* (2014a). <http://iopscience.iop.org/article/10.1088/1748-9326/9/10/105001/meta>. Licensed under CC-BY 3.0.

Many freshwater HAB that have been described as spectacular or extreme have been documented worldwide in the past two decades. An example of freshwater bloom expansion is in Lake Tai (or Taihu), China, where blooms of the toxigenic cyanobacterium *Microcystis* have increased in duration from ~1 month per yr to nearly 10 months per yr over the past 15 years (Duan *et al.*, 2009), concomitant with increasing fertilizer use in the watershed or other nutrient sources (Glibert *et al.*, 2014a; Figure 1.1). As other examples, over roughly the past decade, toxic *Microcystis aeruginosa* blooms, easily visible from satellite imagery, have expanded to cover the entirety of Lake St. Clair (Michigan and Ontario, Canada; ~1114 km<sup>2</sup> or 430 mi<sup>2</sup>) and much of Great Lake Erie (surface area, ~25,745 km<sup>2</sup> or 9940 mi<sup>2</sup>) (Michalak *et al.*, 2013; NOAA, 2015; ESA, 2016). In August 2014, the city of Toledo, Ohio, issued a “Do not drink or boil” advisory to about 500,000 people after microcystins in the city’s finished drinking water were measured at up to 2.5 µg L<sup>-1</sup> (Fitzsimmons, 2014). *Microcystis* blooms have become common features in Florida’s major river systems, the St. Johns and Caloosahatchee; in Lake Okeechobee (the tenth largest lake in the United States; surface area, 1714 km<sup>2</sup> or 662 mi<sup>2</sup>); and in the freshwater tidal St. Lucie Estuary, where huge outbreaks have been visible from satellite imagery and have been sustained seasonally every year over the past decade (Neuhaus, 2016). Although these and other freshwater HAB have been most often linked to P enrichment (e.g., Schindler *et al.*, 2016, and references therein), it is now recognized

that failure to “co-manage” N along with P can be an important factor controlling the magnitude and toxicity of these blooms (Burkholder and Glibert, 2013, and references therein; Monchamp *et al.*, 2014; Glibert *et al.*, 2014a, 2017; Harris *et al.*, 2016).

These examples alone are reason to link the global expansion of some HAB with the expansion of nutrient loads. However, such examples do not fully explain why certain HAB species proliferate and often become the dominant algae, nor do these examples convey the full extent of anthropogenic changes affecting the habitat of these species. What is clear is that the historic view of phytoplankton responses to eutrophication – increased nutrients promote increased chlorophyll and high-biomass blooms, leading to oxygen deduction and losses in habitat (e.g., Cloern, 2001) – is too simplistic for understanding how many harmful algal species respond to changes in nutrients. Anthropogenic activities occurring worldwide are altering landscapes, seascapes, and atmosphere-scapes in complex ways, and the responses by the resident community are equally complex. The complexities of “being there” are next addressed.

### 1.3.2 Resource Ratios, Nutrient Stoichiometry, and Optimal Nutrient Ratios

Resource ratio theory (Tilman, 1977, 1982, 1985; Smayda, 1990, 1997b) predicts that as the ratios of

different essential elements change, the assemblage structure will change due to competition between algae with different optimal nutrient ratios. The “optimum” N:P is the ratio of the values where the cell maintains the minimum N and P cell quotas (Klausmeier *et al.*, 2004). Changes in this ratio have been compared to shifts in phytoplankton assemblage composition, yielding insights about the dynamics of nutrient regulation (e.g., Tilman, 1977; Smayda, 1990; Hodgkiss and Ho, 1997; Hodgkiss, 2001; Heil *et al.*, 2007; Glibert *et al.*, 2012). Perhaps the clearest demonstration of the effect of altered nutrient supply ratios involves the stimulation of non-diatom species following changes in the availability of N or P relative to silica (Si). Diatom species, which mostly are beneficial, require Si in their cell walls, whereas most other phytoplankton do not. They must sequester major amounts of hydrated Si from the surrounding water for their cell wall formation (Sullivan *et al.*, 1981). As N and P have increased from anthropogenic inputs, the relative proportion of Si has changed. Since Si is not abundant in sewage effluent like N and P, the N:Si or P:Si ratios in many lakes and reservoirs, rivers, estuaries, and coastal waters have increased over the past several decades as human populations have increased (Schelske *et al.*, 1986; Smayda, 1989, 1990; Rabalais *et al.*, 1996). Changes in Si availability have also occurred due to sediment trapping (which would include cell walls of dead diatoms, from which Si is very slowly dissolved) and elemental transformations following construction of dams (e.g., Billen *et al.*, 1999; Vörösmarty *et al.*, 2003; Beusen *et al.*, 2005; Syvitski *et al.*, 2005; see also Section 4.2). Diatom growth declines when hydrated Si availability declines, but other phytoplankton groups that do not need Si can continue to proliferate by using the excess N and P.

Among changes in various nutrient ratios, changing N:P ratios have received considerable attention because of the magnitude of the anthropogenic changes that have occurred due to N and P loading on the one hand, and efforts to reduce nutrient loads on the other. Differences in application rates, together with differences in soil retention of P compared to N, and management efforts that generally have emphasized reductions in P loading relative to N, have led to increasingly skewed N:P ratios in anthropogenic nutrient loads. In many parts of the developed world, reductions mostly in P (e.g., in sewage effluents and laundry detergents; Litke, 1999; Stow *et al.*, 2001; Alexander and Smith, 2006) have been undertaken in attempts to reduce or control algal blooms. The

consequence is that many receiving waters are now not only enriched with nutrients, but also these nutrients are in proportions that differ markedly from the proportions of decades past – and also diverge considerably from those that have long been associated with healthy phytoplankton growth, namely, Redfield proportions (Glibert and Burkholder, 2011). It has also been estimated that the atmospheric deposition of nutrients in the ocean is now ~20 times the Redfield ratio for N:P (Jickells, 2006; Peñuelas *et al.*, 2012). The N:P stoichiometry has also markedly shifted in freshwater systems (Elser *et al.*, 2009; Glibert *et al.*, 2014a; Harris *et al.*, 2016). Such changes in the N:P stoichiometry of nutrient supplies have major consequences for HAB.

Various surveys of optimal N:P molar ratios across a broad range of phytoplankton groups have revealed that, while the data tend to cluster around the Redfield ratio (Redfield, 1934), there are numerous examples at both the high and low ends of the spectrum (e.g., Hecky and Kilham, 1988; Geider and La Roche, 2002; Klausmeier *et al.*, 2004). Some analyses even indicate that “Redfield ratios are the exception rather than the rule” in freshwaters (Hecky *et al.*, 1993). Different taxonomic groups (e.g., phyla or classes) of microalgae, and even different species within the same genus, have been shown to have distinct ecophysiological characteristics with respect to nutrient requirements. Given that microalgae span many orders of magnitude in cell volume, from <2 μm to more than 4000 μm, it should not be surprising that the elemental demands of different types of microalgae vary (Harris, 1986; Chisholm, 1992; Geider and LaRoche, 2002; Finkel *et al.*, 2010; and references therein). In a meta-analysis of both freshwater and marine studies of phytoplankton stoichiometry, Hillebrand *et al.* (2013) confirmed that phytoplankton N:P ratios become more restricted and lower with increasing growth rate, and that at maximum growth rate N:P converges to an optimal ratio (or a more narrowly defined range) that differs depending on the species and phylogenetic group. The weighted molar averages for optimal N:P ratios appear to be lowest for diatoms (14.9), increase for dinoflagellates (15.1), and increase even more for cyanobacteria (25.8) and chlorophytes (27.0; Hillebrand *et al.*, 2013).

Algal taxa have different optimal nutrient ratios for various reasons. They may have a lower overall requirement for a particular nutrient. Very small cells, such as picocyanobacteria, have a lower requirement for P due to the smaller

need for structural components in the cell (Finkel *et al.*, 2010). Alternatively, or additionally, species that thrive under such conditions may have the ability to “make do with less” by physiological substitution of a P-containing compound(s) with a non-P-containing compound(s), as in the case of substitution of a P-containing lipid with a non-P-containing lipid (sulfolipid). Many cyanobacteria appear to have this capability (Van Mooy, 2009). Thus, the cellular carbon (C):P content of *Synechococcus*, for example, is about 100, whereas that of a typical diatom is about 50 (Finkel *et al.*, 2010). Many HAB species also can upregulate their ability to acquire a particular nutrient if and when it becomes available. As an example, gene expression has been reported for cultured *Microcystis* under conditions of extremely low P; two high-affinity, P-binding proteins and alkaline phosphatase were strongly upregulated by factors of 50- to 400-fold (Harke *et al.*, 2012; Gobler *et al.*, 2016).

Alterations in the composition of nutrient loads have been correlated with shifts from diatom-dominated to flagellated-dominated algal assemblages in many regions. Continuing with the example of China introduced above, in the Huanghai Sea region, inorganic N:P ratios are now about twice Redfield proportions, and about fourfold higher than in the 1990s (Ning *et al.*, 2009; Glibert *et al.*, 2014a). In that region, there has also been nearly a sixfold increase in HAB occurrences and a shift to proportionately more dinoflagellates in comparison to diatoms (Fu *et al.*, 2012a; Glibert *et al.*, 2014a). Similarly, in the South China Sea region, water-column inorganic N:P ratios increased from  $\sim 2$  in the mid-1980s to  $>20$  in the early 2000s (Ning *et al.*, 2009). In addition to the increase in the number of HAB, a shift in species composition to increasing dominance of genera such as *Chattonella*, *Karenia*, and *Dinophysis* has occurred (Wang *et al.*, 2008).

Nutrient stoichiometry has been shown to be strongly related to blooms of pelagic *Prorocentrum* species (Glibert *et al.*, 2012), but in a manner that changes with the growth state of the bloom. Planktonic *Prorocentrum* blooms are often initiated at N:P levels below Redfield, stimulated by a “flush” of nutrients or organic materials (i.e., by nutrients “getting there” from a run-off or other delivery event). As examples, blooms of *P. minimum* in the Baltic Sea and Chesapeake Bay are characteristically initiated following a flush of organic nutrients (Granéli *et al.*, 1989; Glibert *et al.*, 2001), while blooms of *P. donghaiense* in the East China Sea

likely are initiated by an injection of P-rich water from the Taiwan Warm Current and its intersection with N-rich Changjiang River plume water (Tang *et al.*, 2000; Fang, 2004; Zhou *et al.*, 2008; Li *et al.*, 2009). Once the growth rate increases, bloom biomass is able to increase, often reaching nearly monospecific proportions at N:P ratios much higher than Redfield. After the blooms are established, they apparently can be maintained at substantially elevated N:P levels for long periods through mixotrophy or other adaptive strategies that allow balance of cellular nutrients and energy in an environment where nutrients are provided in imbalanced proportions (Glibert *et al.*, 2012, and references therein). Examples of such high-biomass blooms maintained with N:P in excess of Redfield proportions have been reported in the Baltic Sea (Hajdu *et al.*, 2005), the Delaware Inland Bays (Handy *et al.*, 2008), the Neuse River Estuary (Springer *et al.*, 2005), the East China Sea (Li *et al.*, 2009), and Chesapeake Bay (Li *et al.*, 2015). Thus, while high growth rates may enable initiation of blooms, adaptive physiology may allow blooms to be maintained, that is, to “be there” at less than maximal growth rates and at non-optimal N:P ratios. Accoroni *et al.* (2015) applied a similar conceptual model of N:P regulation for blooms of the benthic dinoflagellate *Ostreopsis cf. ovata* in the northern Adriatic Sea.

An intriguing curiosity, and one that goes *against* the prevailing notion that HAB occur in response to nutrient enrichment, is the observation that some HAB appear to occur more frequently following reductions, rather than increases, in nutrient pollution. Several specific types of HAB seem to illustrate this phenomenon, such as *Alexandrium* spp. that produce paralytic shellfish toxin. The most commonly cited example of this phenomenon is the Seto Inland Sea, Japan, where nutrient loads were significantly reduced following sewage upgrades. While overall numbers of blooms and their biomass declined, outbreaks of *Alexandrium tamarense* and *Alexandrium catenella* became more prevalent (Anderson *et al.*, 2002). A similar observation was reported from the Thau Lagoon, southern France (Collos *et al.*, 2009). These types of events may be examples of HAB that are promoted not only by nutrient availability but also by changing nutrient proportions. In both cases, P reductions were imposed without concurrent reductions in N, leading to an elevated N:P condition. Overall, it is not necessarily the total nutrient pollutant load that causes HAB, but the change in the composition of those nutrients.



### 1.3.3 Diversity in Use of Forms of Nitrogen

In addition to nutrient ratios that promote species with a higher or lower requirement for a particular nutrient, the *form* in which the nutrient is supplied may also control whether a specific nutrient load will promote a HAB. Organic nutrients have been shown to be important in the development of blooms of various HAB species, in particular cyanobacteria and dinoflagellates (e.g., Paerl, 1988; Glibert *et al.*, 2001), and the importance of organic nutrient forms in blooms is increasingly recognized worldwide (e.g., Granéli *et al.*, 1985; Berg *et al.*, 1997, 2003; Berman, 1997; Berman and Bronk, 2003; Glibert and Legrand, 2006; Collos *et al.*, 2014). For example, cyanobacterial blooms in Florida Bay and on the southwest Florida shelf have been shown to be positively correlated with the fraction of N taken up as urea, and negatively correlated with the fraction of N taken up as  $\text{NO}_3^-$  (Glibert *et al.*, 2004). A substantial body of literature suggests that diatoms are  $\text{NO}_3^-$  specialists (e.g., Lomas and Glibert, 1999a, 1999b; Figueiras *et al.*, 2002; Kudela *et al.*, 2005), while cyanobacteria, and many chlorophytes and dinoflagellates, may be better adapted to use of  $\text{NH}_4^+$ , urea, or other organic N forms (see reviews by Collos and Harrison, 2014; Glibert *et al.*, 2016). Such differences are consistent with differing evolutionary lineages of these groups, and with increasing insights about the physiology of these different functional groups (Wilhelm *et al.*, 2006; Glibert *et al.*, 2016, and references therein).

The importance of organic N forms is increasingly recognized in algal nutrition, especially in HAB proliferation (Berg *et al.*, 1997; Berman and Bronk, 2003; Bronk *et al.*, 2007; Glibert and Legrand, 2006, and references therein). The pathways by which osmotrophy occurs are numerous, and include direct uptake as well as extracellular oxidation and hydrolysis (Glibert and Legrand, 2006, and references therein). Enzymatic measurements have been used to determine some of the pathways involved in the incorporation and degradation of organic compounds (Chróst, 1991). Urease activity appears to be constitutive for many algal species, but may be higher in many HAB species compared to non-HAB (e.g., Fan *et al.*, 2003; Lomas, 2004; Solomon *et al.*, 2010). For example, urease activity is sufficiently high in *Aureococcus anophagefferens* and *P. minimum* to meet the cellular N demand for growth, but seemingly insufficient to meet the N growth demand for the diatom *Thalassiosira weissflogii* (Fan *et al.*,

2003). In *Alexandrium fundyense*, urease activity was shown to be seasonally variable and positively related to the toxin content of the cells (Dyhrman and Anderson, 2003). Both peptide hydrolysis and amino acid oxidation may be important in some HAB, as shown by Mulholland *et al.* (2002) in studies of *A. anophagefferens* in natural communities. Leucine amino peptidase is another protease that hydrolyses peptide bonds and liberates amino acids (Langheinrich, 1995; Dyhrman, 2005). It is measured by assessing the rate of hydrolysis of an artificial substrate, and has been shown to be of potential significance in dinoflagellates and other HAB classes (Berges and Falkowski, 1996). Stoecker and Gustafson (2003), for example, demonstrated in Chesapeake Bay that leucine aminopeptidase activity was associated with a dinoflagellate bloom, and that in non-axenic cultures of *Akashiwo sanguinea*, *Gonyaulax grindley*, *Gyrodinium uncatenum*, *Karlodinium micrum*, and *P. minimum*, the activity was associated with the dinoflagellates and not the bacteria.

Cyanobacteria, especially picocyanobacteria, have differing abilities to take up and assimilate  $\text{NO}_3^-$  and  $\text{NH}_4^+$  (e.g., Flores and Herrero, 1994; Harris *et al.*, 2016). Even for the picoplankton cyanobacteria that do not include  $\text{N}_2$ -fixers, there is wide diversity in their ability to use  $\text{NO}_3^-$  or  $\text{NH}_4^+$  (Scanlan and Post, 2008, and references therein). Some picocyanobacteria cannot take up  $\text{NO}_3^-$  at all (Moore *et al.*, 2002; Rocap *et al.*, 2003), while some can take up both  $\text{NO}_3^-$  and  $\text{NO}_2^-$  (Martiny *et al.*, 2009). Many cyanobacteria have constitutive expression of high-affinity  $\text{NH}_4^+$  transporters at the cell membrane (Wilhelm *et al.*, 2006, and references therein).

Many experiments have shown that a different algal assemblage can develop when the form of N is altered, even holding the same total N constant and/or at levels that are seemingly saturating for uptake or growth. Early mesocosm experiments by Glibert (1998) showed that different size classes of phytoplankton develop when the proportion of  $\text{NO}_3^-$  to  $\text{NH}_4^+$  varies: a doubling in the ratio of the ambient  $\text{NO}_3^-$  to  $\text{NH}_4^+$  resulted in a nearly 50% increase in the ratio of  $>10\ \mu\text{m}$  to  $<10\ \mu\text{m}$  sized algal biomass. In laboratory mesocosm experiments conducted with nutrient-rich water from the Choptank River (a tributary of Chesapeake Bay), Glibert and Berg (2009) showed that  $\text{NO}_3^-$  uptake was directly related to the fraction of the assemblage as diatoms, while the proportion of  $\text{NH}_4^+$  uptake was directly proportional to the fraction of the assemblage as cyanobacteria. Donald *et al.* (2011, 2013) also found, in experiments

conducted in freshwater lakes in Canada, that  $\text{NO}_3^-$  enrichment led to a proportionately greater increase in chlorophyll-*a* (relative to total wet-weight algal biomass) and a greater initial response by diatoms, while  $\text{NH}_4^+$  enrichment led to a proportionately greater increase in cyanobacteria. In experiments conducted in the San Francisco Bay Delta, Glibert *et al.* (2014b) reported proportionately more chlorophyll-*a* and more diatoms in a low-light regime when the N enrichment substrate was  $\text{NO}_3^-$ , while more cyanobacteria developed in a high-light regime when  $\text{NH}_4^+$  was provided as the enrichment substrate in the same concentration. Domingues *et al.* (2011) also showed that enrichment by  $\text{NH}_4^+$  in a freshwater tidal estuary favored chlorophytes and cyanobacteria, whereas diatoms were favored under  $\text{NO}_3^-$  enrichment. The same trends additionally were reported for the phytoplankton assemblage in highly eutrophic Anacostia River water (a tributary of Chesapeake Bay); when experimentally enriched with  $\text{NH}_4^+$ , a proportionately greater response by cyanobacteria and chlorophytes was observed relative to enrichment of samples with the same amount of  $\text{NO}_3^-$ , which elicited a greater diatom response (Jackson, 2016).

Toxic cyanobacteria species also appear to be favored over diatoms when N is supplied in chemically reduced forms relative to oxidized forms – as, for example, in the hypereutrophic Lakes Taihu, China, and Okeechobee, Florida, United States (McCarthy *et al.*, 2009). Harris *et al.* (2016) reported that cyanobacterial biomass increased in midwestern lakes when the proportion of  $\text{NH}_4^+$  relative to  $\text{NO}_3^-$  increased. Numerous field studies have shown that dinoflagellates, many of which are HAB formers, are also associated with increased proportion of N in chemically reduced (e.g.,  $\text{NH}_4^+$  and urea) rather than oxidized forms (e.g.,  $\text{NO}_3^-$  and  $\text{NO}_2$ ; Berg *et al.*, 2003; Glibert *et al.*, 2006; Heil *et al.*, 2007). Thus, as for terrestrial plants, there is a dichotomy in use of oxidized versus reduced N forms, and differential optimal N:P ratios for different phytoplankton functional groups, the end result of which is an altered phytoplankton assemblage composition when nutrient loads, ratios, and forms are altered (Glibert *et al.*, 2016, and references therein; Figure 1.2).

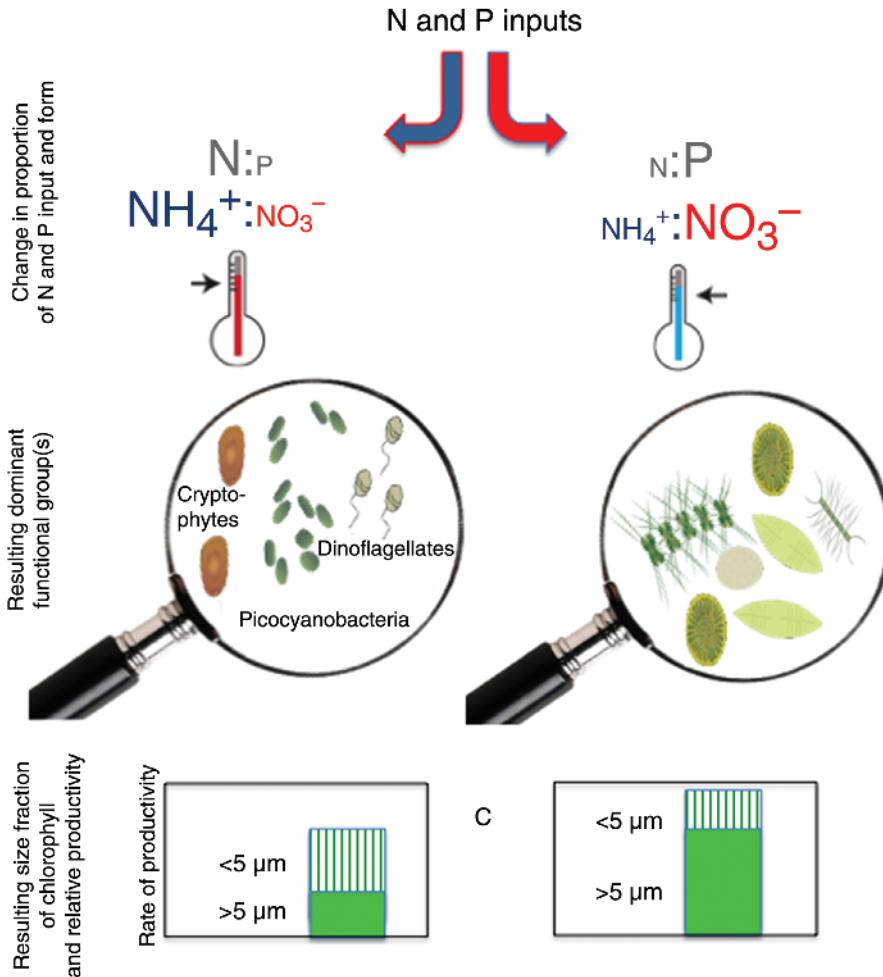
### 1.3.4 Toxicity

Considerable emerging evidence has shown that nutrient proportions and forms have effects on

toxin production as well growth of HAB (e.g., Béchemin *et al.*, 1999; Corcoran *et al.*, 2014). Many toxic algae increase in toxin content under conditions of elevated N:P ratios (e.g., Granéli *et al.*, 1998; Granéli and Johansson, 2003; Granéli and Flynn, 2006; Hardison *et al.*, 2012, 2013). Many toxins are rich in N as well as C, and thus production of toxins might be considered as a dissipatory mechanism whereby cells release the N or C not needed in metabolism (Glibert and Burkholder, 2011; Glibert *et al.*, 2016). Although not conclusively shown for any toxin, toxin production may be part of the complex suite of physiological processes involved in “overflow metabolism” (*sensu* Glibert *et al.*, 2016).

As examples, under conditions of elevated N:P ratios, hemolytic activity per cell has been shown to increase by up to tenfold in the haptophytes *Prymnesium parvum* and *Chrysochromulina* (now *Prymnesium*) *polylepis* (Johansson and Granéli, 1999). Similarly, at higher N:P ratios, neurotoxin production increased in the diatom *Pseudo-nitzschia multiseries*. Excess N and high N:P ratios have also been related to increased microcystin (MC) production under controlled culture conditions (e.g., Lee *et al.*, 2000; Oh *et al.*, 2000; Vézic *et al.*, 2002; Downing *et al.*, 2005; Van de Waal *et al.*, 2009). As recently reviewed by Gobler *et al.* (2016), common cyanotoxins, including MC, nodularins, cylindrospermopsins, and saxitoxins, have amino acid precursors (glutamine, arginine, or leucine), and they, in turn, depend on adequate N supply for their assimilation (Figure 1.3). An adequate N supply is also needed for assimilation of many dinoflagellate toxins (Dagenais-Bellefeuille and Morse, 2013, and references therein), as has been shown for the dinoflagellates *Karlodinium venificum*, *Alexandrium* sp., and *Karenia brevis* (Granéli and Flynn, 2006; Hardison *et al.*, 2013). In all, the production of metabolites and toxins that contain N tends to be higher when N availability is high, while those that are proportionately more C-rich are more abundant in the cells when N availability is low (Glibert *et al.*, 2016; Harris *et al.*, 2016).

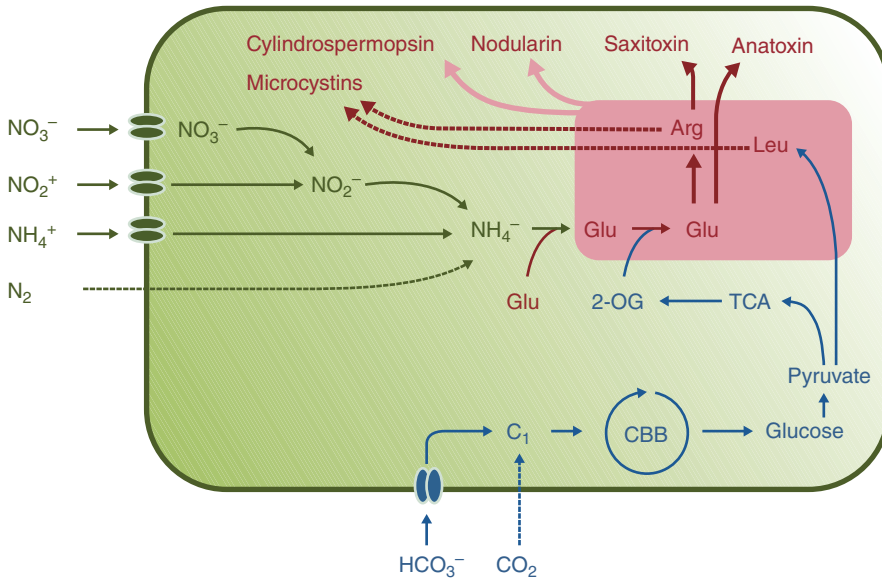
In addition to the proportion of N relative to other elements, the form of N on which cells are growing also affects the synthesis of secondary metabolites, including toxins. Over the growing season of three lakes in Québec known to have toxic cyanobacteria, the cyanobacterial assemblage structure and total MC concentrations of toxins were strongly related to the availability of chemically reduced and organic N forms (DON and



**Figure 1.2** Summary conceptual schematic illustrating the effect of changes in the proportion of nitrogen to phosphorus (N:P), the relationship between  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in N loads, and the temperature regime in a natural system. When the N:P ratio is elevated,  $\text{NH}_4^+$  is the dominant form, and when waters are warmer, flagellates, cyanobacteria, and chlorophytes commonly proliferate, leading to overall productivity dominated by small-sized algae (here,  $<5 \mu\text{m}$ ). In contrast, when the N:P ratio is lower,  $\text{NO}_3^-$  is the dominant form provided, and when conditions are cooler, diatoms are abundant and overall production will likely be dominated by cells of a larger size class (here,  $>5 \mu\text{m}$ ). Moreover, chlorophyll *a* yield and total production may be higher than under the  $\text{NH}_4^+$  enrichment condition. *Source:* Reproduced and modified from Glibert *et al.* (2016). <https://creativecommons.org/licenses/by/4.0/>. Licensed under CC-BY 4.0.

$\text{NH}_4^+$ ; Monchamp *et al.*, 2014). Furthermore, in mesocosm studies, additions of  $\text{NH}_4^+$  led to higher MC concentrations and cyanobacteria blooms of longer duration compared with experiments in which  $\text{NO}_3^-$  was the added N substrate (Donald *et al.*, 2011). Recently, Harris *et al.* (2016) reported that in eutrophic midwestern U.S. reservoirs, the concentration of secondary metabolites including toxins increased under elevated  $\text{NH}_4^+:\text{NO}_3^-$  ratios. In work with cultures of the marine dinoflagellate *A. tamarensis*, additions of  $\text{NH}_4^+$  resulted in higher

cell quotas of toxin than did additions of  $\text{NO}_3^-$  (Leong *et al.*, 2004). Given the extensive research on the differential metabolisms of oxidized versus reduced N in higher plants (e.g., Warnecke and Barber, 1973; Johnson *et al.*, 1984; Nakagawa *et al.*, 1984; Fontana *et al.*, 2006; Praveen *et al.*, 2011, among others), it is not surprising that the proportion of nutrients and their forms have direct effects on the metabolites, including toxins, of microalgae (e.g., Van de Waal *et al.*, 2009, 2014; Montchamp *et al.*, 2014; Downing *et al.*, 2015).



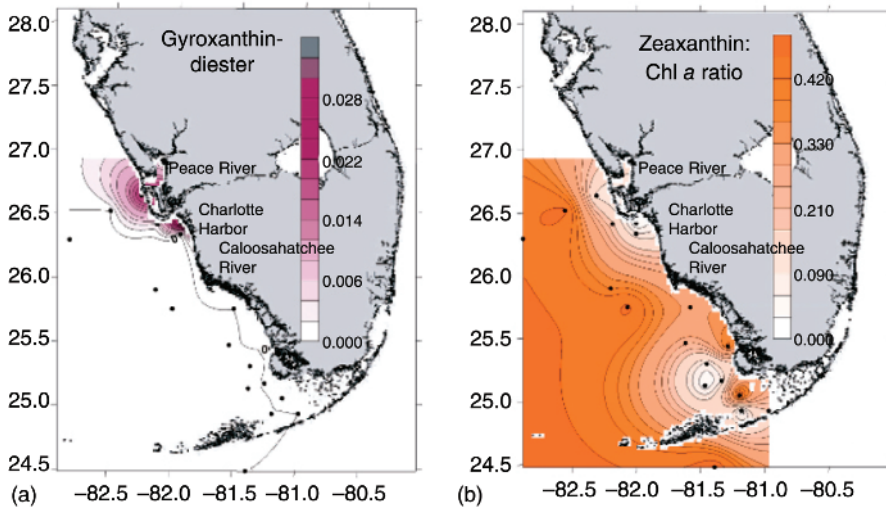
**Figure 1.3** Cell schematic illustrating the relationship between nitrogen (N) and carbon (C) uptake and assimilation into amino acids, and synthesis of major cyanobacterial toxins derived from these amino acids. Ci, cellular inorganic carbon; CBB, Calvin–Benson–Bassham cycle; TCA, tricarboxylic acid; 2-OG, 2-oxoglytarate; Gln, glutamine; Glu, glutamate; Arg, arginine; Leu, leucine. *Source:* Modified after Van de Waal (2010) and reproduced from Gobler *et al.* (2016) with permission of Elsevier.

### 1.3.5 Mixotrophy: Use of “Packaged” and Dissolved Particulate Nutrients

An important advancement in the understanding of HAB and their nutrition over the past decade or so has been the evolving recognition of the importance of mixotrophy in the nutritional ecology of many HAB species, especially those that are prevalent in nutrient-rich environments (Burkholder *et al.*, 2008). Mixotrophy (here, phagotrophy) allows HAB to acquire nutrients in pre-packaged or particulate form; this is recognized as an important strategy when insufficient dissolved nutrients are available in the environment - but it can also be important when the balance of nutrients is unfavorable, regardless of the absolute concentration of the dissolved nutrient (Jeong *et al.*, 2010; Flynn *et al.*, 2013). Essential elements such as N, P, and C are typically rich in microbial prey and, thus, mixotrophy can provide a supplemental supply when there is an elemental imbalance in dissolved (water-column) nutrient substrates (Granéli *et al.*, 1999; Vadstein, 2000; Li *et al.*, 2001; Stibor and Sommer, 2003; Stoecker *et al.*, 2006). In eutrophic environments, although nutrients may be proportionately more available than in oligotrophic environments, nutrients often are out of stoichiometric balance (Burkholder *et al.*, 2008; Burkholder and Glibert, 2013). In the North Sea, for example, as

increasing N relative to P proportions developed in response to disproportionate nutrient reductions, mixotrophic dinoflagellates increased, and many of these were harmful species (Burson *et al.*, 2016). Recent laboratory experiments also have shown that, at least for some mixotrophs, grazing is highly dependent on not only their physiological or nutritional state, but also that of their prey (e.g., Lundgren *et al.*, 2016; Lin *et al.*, 2017).

Mixotrophy also may permit growth to be sustained or even accelerated during periods of apparent water-column nutrient deficiency or imbalance (or real nutrient deficiency for non-mixotrophic competitors) if only inorganic forms of dissolved nutrients are considered. The dinoflagellates *Cochlodinium (Margalefidinium) polykrikoides* and *K. brevis* exemplify these benefits of mixotrophy. When growing as a phototroph, *C. polykrikoides* had a growth rate of 0.17 divisions day<sup>-1</sup> (Jeong *et al.*, 2004). Yet, when grown as a mixotroph with cryptophytes as prey, the division rate of *C. polykrikoides* nearly doubled to 0.34 divisions day<sup>-1</sup> (Jeong *et al.*, 2004). In the case of toxigenic *K. brevis*, grazing can occur on the cyanobacterium *Synechococcus* sp. (Jeong *et al.*, 2005; Glibert *et al.*, 2009). In laboratory experiments, Jeong *et al.* (2005) estimated that 5 cells hour<sup>-1</sup> of *Synechococcus* could be grazed by mixotrophic *K. brevis*, while Glibert *et al.* (2009) found that from ~1 to 80 *Synechococcus*



**Figure 1.4** Contour maps of (a) abundance of the pigment gyroxanthin-diester (indicative of *Karenia brevis*) and (b) zeaxanthin (indicative of cyanobacteria such as *Synechococcus*) relative to chlorophyll-*a* for the southwestern Florida shelf, sampled in May 2013. Source: Reproduced and modified from Heil *et al.* (2007) with permission of Wiley.

cells hour<sup>-1</sup> were grazed by *K. brevis*, depending on the predator–prey ratio. The growth rate of *K. brevis* increased as the supply of *Synechococcus* increased, indicating that natural variability in this food source may affect growth rates of this HAB species in nature. On the western Florida shelf, an inverse relationship between the spatial extent of *K. brevis* (as measured by the indicator pigment gyroxanthin-diester) and picocyanobacteria (as measured by the indicator pigment zeaxanthin and confirmed microscopically) suggested that mixotrophic grazing contributed to the lower abundance of picocyanobacteria near Charlotte Harbor and the Caloosahatchee River plume (Heil *et al.*, 2007; Figure 1.4). At the very least, availability of a food source may help to sustain the HAB after inorganic nutrient supplies have been diminished.

Jeong *et al.* (2010) described these trophic interactions as serving as “hubs” (in the sense of an airport hub) for energy and nutrient flow through the microbial consortium. Species such as *Prorocentrum* spp. can dominate a hub, serving as both predator and prey of a wide range of species. Such a designation has particular relevance when these species become dominant in a phytoplankton assemblage. The “hub” serves to concentrate nutrients and to transfer them to higher trophic levels. Thus, in addition to providing a growth benefit for HAB species, mixotrophy may provide a physiological mechanism for acquisition of a nutrient that may not be available in dissolved form, and therefore would not be available to competitors without alternate nutrition strategies.

This complexity in response to nutrient proportion and form challenges the commonly held notion that nutrients are only regulating when they are in limiting proportions (e.g., Reynolds, 1999; Davidson *et al.*, 2012, 2014; Wells *et al.*, 2016). Mixotrophy is a common mechanism or “strategy” in waters where nutrients are not stoichiometrically balanced – a condition often enhanced by anthropogenic changes in N relative to P (or Si). Importantly, nutrient limitation does not need to be imposed for stoichiometric imbalanced conditions to develop. Properties of cells such as enzyme activities, gene regulation, cellular pigmentation complement, cell elemental composition, and toxin content all vary across the entire gradient of nutrient supply, not just the limiting range. Thus, as anthropogenic activities change not only the total amount but also the gradient and form of nutrient supply, organisms, including harmful algal species, respond accordingly. The perpetuation of the classic view that nutrient must be in limiting concentration levels to control algal biomass has been a major hindrance in understanding how the composition of algal assemblages changes; nutrient form and proportion have consequences for ecosystem structure and function, whether nutrients are limiting or not.

### 1.3.6 Other Adaptations

In addition to these strategies for nutrient acquisition, other adaptations can provide benefit to

some HAB species under altered nutrient conditions. Many of these species are flagellates that can swim (while diatoms do not) and exhibit vertical migration behavior. They can move into deeper, more nutrient-rich waters, especially toward the microbially active pycnocline or the sediment–water interface. Under certain environmental conditions, their swimming behavior may result in the formation of high-density patches (e.g., Franks, 1992; Kamykowski *et al.*, 1998). Some cyanobacterial species can similarly regulate their vertical position in the water column by synthesis and collapse of gas vesicles inside their cells (Walsby, 1975). Vertical movement by cells in a stratified environment may help to maximize encounter frequencies for sexual reproduction (for eukaryotic microalgae), minimize grazing losses, and allow cells to obtain nutrients at depth and light at the surface. Some unicellular species form mucilaginous colonies that can impede grazers and/or protect species from viral or bacterial infection (Lancelot *et al.*, 2002).

Furthermore, many harmful algae have benthic cysts or other resting stages that enable cells to withstand hostile or unfavorable environmental conditions. The metabolic switch from resting stages to motile stages often is generally synchronized for an algal population (Kremp, 2001; Vahtera *et al.*, 2014), and the actively dividing cells initiate a bloom. These cysts or spores provide a recurrent seed source or inoculum for planktonic populations, and this characteristic may be a critical factor in determining not only the geographic distribution of species but their eventual abundance as well. All of these behaviors have important implications for harmful algal species success, and serve to underscore the deep complexity of the biology of these seemingly “simple” organisms; there are clearly many factors contributing to harmful species “being there.”

## 1.4 “Staying There”: Links to Physical Structure and Climate

### 1.4.1 Physical Structure: Large-Scale and Small-Scale Natural Hydrological Features

Physical factors influence both nutrient retention and cell retention. Hydrological features such as residence time and turbulence select for various taxa (e.g., Anderson, 1998; Hallegraeff and Fraga,

1998). A major question in HAB biogeography is whether there are biotic provinces that are conductive for specific types of HAB species. Indeed, there are many examples of recurrent HAB in specific biomes, and a few such examples are highlighted here. Highly dynamic estuaries typically have a phytoplankton assemblage distinct from that in quiescent coastal lagoons. The former is more often dominated by diatoms, the latter often by picoplankton such as picocyanobacteria, as in the case of Florida Bay, or pico-pelagophytes, such as “brown tides” *Aureococcus anophagefferens* in Narragansett Bay, Rhode Island; Great South Bay, New York; and the Maryland Coastal Bays, and *Aureoumbra lagunensis* in Laguna Madre, Texas (Buskey *et al.*, 1997; Glibert *et al.*, 2010, and references therein).

It is now well recognized that HAB are a regular and fundamental feature of upwelling marine systems (e.g., Margalef, 1978; Pitcher *et al.*, 2005, 2010; Pitcher and Weeks, 2006). Upwelling may impact coastal phytoplankton blooms and drive new production, but importantly, depending on the coastal configuration, there may be sites where an oceanic supply of nutrients, coupled with terrestrial sources of nutrients and retention zones, may concentrate blooms. Generally, the seasonal succession of microalgae in upwelling systems mirrors that of most temperate systems, with spring diatoms giving way to increasing contribution of dinoflagellates by late summer/early fall (Pitcher *et al.*, 2005, 2010). As an example, the regularity of seasonal transitions between upwelling and downwelling favorable conditions, and the seasonal succession of HAB, has been shown for the Galician coast. There, chain-forming diatoms, including toxic *Pseudo-nitzschia* spp., dominate spring and summer upwelling events when N species are dominated by  $\text{NO}_3^-$ , but as summer progresses during stratified conditions, dinoflagellates, and particularly the genera *Ceratium*, *Dinophysis*, *Protoperidinium*, *Gymnodinium*, *Gyrodinium*, and *Prorocentrum*, increase in abundance as the N species shift to more regenerated forms (Figueiras and Rios, 1993; Moita, 2001). By the end of summer, heterotrophic dinoflagellates (e.g., *Noctiluca scintillans* and *Mesodinium rubrum*) are increasingly present (Cabeçadas *et al.*, 1983). Finally, blooms of efficient swimmers, including the toxigenic chain-forming dinoflagellate *Gymnodinium catenatum*, occur during the upwelling–downwelling transition (Moita *et al.*, 1998).

As summarized by Pitcher *et al.* (2010), coastal upwelling contributes to the enrichment of surface waters and high productivity, and also contributes

to the transport or export of production from the shelf and coastal regions (Largier *et al.*, 2006). Coastal features such as banks, canyons, or islands have influences on upwelling and its local spatial effects. This is exemplified in the effects of local coastline on blooms in the Santa Barbara Channel. In this region, there are various oscillations of upwelling, relaxation, and convergence. At times these features can form eddies that concentrate plankton (Nishimoto and Washburn, 2002), including HAB. The formation of such eddies, following local upwelling in the Santa Barbara Channel, strongly influences the distribution and toxicity of blooms of *Pseudo-nitzschia* spp., moving the most toxic cells to the center of the eddy (Anderson *et al.*, 2006). Similarly, in the northern California Current system, the Juan de Fuca eddy, a cold, cyclonic gyre located over the continental shelf near the mouth of the Juan de Fuca Strait is associated with advection of nutrient-rich water to the surface by estuarine circulation. The eddy, which increases over the course of the summer as the California undercurrent water is upwelled, is characterized by enhanced phytoplankton biomass and has been implicated as a site for the initiation of toxic *Pseudo-nitzschia* affecting the Washington coast, particularly during summer and autumn (Trainer *et al.*, 2002, 2009). These toxic blooms only impact coastal environments when subsequent downwelling favorable conditions exist, allowing the toxic cells to exit the eddy and to be advected onshore (MacFayden *et al.*, 2005).

Small-scale turbulence and stratification also can play important roles in bloom aggregation, especially in regions offshore, away from shallow waters where tidal mixing and wind mixing dominate. HAB often occur when such systems are highly stratified, in some cases at the very smallest of scales. Subsurface layers of HAB have often been reported in highly stratified waters, wherein the HAB cells accumulate at the intersection of light and nutrients. With a source of light from above and nutrients from below, the subsurface layer provides a habitat where both resources are low but neither inhibits growth. Thin layers, in some cases only centimeters to meters thick in the ocean water column, can be sites of dense HAB aggregations. Bjørnsen and Nielsen (1991) described a “magic carpet” of *Gyrodinium aureolum*, while Gentien *et al.* (1995) noted that some thin layers have up to 100% dominance of dinoflagellates.

In addition to the physical aggregation of cells in stratified systems, and especially within thin layers, such layers also provide unique microhabitats for

HAB. These microhabitats are often reducing environments (Wang *et al.*, 2015); thus, chemically reduced forms of N are more prevalent than oxidized forms of N. Heterotrophic nutrition is also common in species that dominate thin layers. *Dinophysis*, for example, depends on mixotrophy. There can also be microstructure in the layers. In the thin-layer structure of the Bay of Biscay, for example, it was shown that one layer consisted of *Chaetoceros sociale* and a second layer consisted of *Dinophysis acuminata* (Lunven *et al.*, 2005). Thus, HAB species are capable of finding habitats in which their adaptations are advantageous for acquiring the specific nutrients they need and prefer.

#### 1.4.2 Physical Dynamics: Anthropogenic Hydrological Changes

In addition to natural hydrological features such as upwelling, anthropogenic activities are altering hydrology in many regions. River discharge is changing throughout the world due to dam construction and other in-river consumptive uses. Dams capable of generating more than 1 megawatt electricity that have been constructed, or are under construction, number in the thousands (Zarfl *et al.*, 2015), and extremely large dams (capable of generating >1 gigawatt) are primarily located in Asia along the Changjiang River Basin (e.g., the Three Gorges Dam), and along the Amazon Basin. These dams have significant and complex effects on river flow and accordingly on environmental conditions conducive to HAB. In addition to the reductions in overall river flow that occur from dam construction (and their associated reservoirs), large river systems with dams can become fragmented, preventing free movement of organisms, and severe modification of river flow alters temperature regimes, dramatically reduces sediment transport (Vörösmarty *et al.*, 2010; Lehner *et al.*, 2011; Liermann *et al.*, 2012), and alters nutrient loads and proportions in downstream waters. For example, retention of Si upstream following construction of the Three Gorges Dam in China has been considered an important factor leading to altered nutrient proportions favoring HAB in the East China Sea (e.g., Zhang *et al.*, 2015).

In the United States, where dam construction is no longer accelerating and in fact is declining, critical issues of upstream consumption versus downstream flow and effects on microbial biodiversity are increasingly argued in court (e.g., Pillion, 2014). Reductions in flow due to upstream

consumption in that case have been related to reductions in overall nutrient loads to the downstream estuary, leading to altered phytoplankton assemblage composition including increased abundance of picocyanobacteria and some HAB at the expense of diatoms (Viveros Bedoya, 2014). Estuarine flow is also highly regulated in the San Francisco Bay Delta (Kimmerer, 2002; Winder *et al.*, 2011; Glibert *et al.*, 2011), and strong, bivariate correlations have been reported between flow and organisms of all levels in the food web. In that estuary, sufficient flow is rigorously maintained through strictly established flow criteria in order to increase the low-salinity habitat for endangered fish. Of particular significance is that over the past several decades (prior to the drought beginning in 2013), the phytoplankton assemblage of the Bay Delta shifted from large diatoms, which were common up to the mid-1970s, to smaller flagellates and cyanobacteria since the mid-1980s (Lehman *et al.*, 2005, 2008; Brown, 2010; Glibert *et al.*, 2011), as a consequence of managed flow, increased pollution by N, and altered grazing communities. Important lessons emerge from both examples: altered flow can change the export of nutrients in terms of total loads and proportions, and these changes can create “windows of opportunity” for HAB to develop or at least create conditions where phytoplankton assemblages shift in composition.

### 1.4.3 Reinforcing Feedbacks

#### 1.4.3.1 Trophic Disruptions

Harmful algal species can also proliferate because of grazing failure, assuming that physicochemical factors (such as nutrients, salinity, light, and temperature) are favorable (e.g., Buskey *et al.*, 1997; Hart, 2006; Kang *et al.*, 2015; Smayda, 2008). Recent work by Harvey and Menden-Deuer (2012), for example, documented fleeing behavior by the toxigenic raphidophyte *Heterosigma akashiwo* in response to a ciliate predator and predation-derived cues, wherein predator-induced changes in the HAB species movements led to a reduction in encounter rate and a threefold increase in net algal population growth rate. Such behaviors that significantly reduce predation pressure were suggested as a new mechanism for HAB formation.

Bakun and Broad (2003) suggested that “loop-holes” in the fields of biological control organisms can result from disruptive environmental perturbations, and this may lead to highly successful recruitment of different species. Building on this

idea, Irigoien *et al.* (2005, p. 313) proposed that perturbations in factors such as nutrients and light alter the microbial loop, whereby the harmful algal species can escape predation pressure and form blooms. Using data on phytoplankton and microzooplankton (ciliates and heterotrophic dinoflagellates) biomass from 12 geographic regions, they proposed that HAB can escape microzooplankton control through predation avoidance mechanisms (e.g., larger size, colonies, spines, and toxins) at bloom initiation. Total exclusion from grazing is not required; only a disparity of grazing rates is needed, so that the harmful algal species attains positive net growth while other phytoplankton remain under grazing control. In support of this notion, Mitra and Flynn (2006) reported that HAB can develop through a “self-propagating failure of normal predator-prey activity, resulting in the transfer of nutrients into HAB growth at the expense of competing algal species.” The rate limitation of this nutrient transfer provides continual nutrient stress that results in various grazing-deterrent behaviors by the harmful species, protecting them from grazing control. This process can be self-stabilizing as long as nutrient demand exceeds supply, which would be most likely under eutrophic conditions with skewed nutrient ratios.

Many HAB also cause subtle, indirect, or complex changes to food webs and trophic interactions. For example, toxicity or allelopathy may serve as an inhibitor of competitors and prey, allowing organisms that would not otherwise have a growth benefit to thrive without competition. Of course, the most notable effect on food webs is fish kills that many harmful algal species can cause through toxicity, gill clogging, and/or oxygen depletion. Direct toxic effects on grazers of a wide range of HAB species have been documented. As examples, toxins from *Karenia mikimotoi* can inhibit zooplankton grazing and growth of competing algae (e.g., Hansen, 1995; Gienten, 1998). In the toxigenic haptophyte *Prymnesium parvum*, the cellular toxins also poison or deter grazers (Granéli and Johansson, 2003), thereby decreasing grazing rates and, in turn, positively influencing growth of the toxic algae. Chapter 7 of this volume describes the food web effects of HAB in detail; here, the point is emphasized that as a HAB becomes established, changes in the food web may contribute to conditions promotive of further HAB maintenance.

Various disruptions of trophic interactions caused by HAB are well documented (e.g., Sunda *et al.*, 2006, and references therein). If such



disruptions lead to reductions in grazing, the bloom taxa can be maintained at a lower growth rate since compensation for grazing loss is not needed. As examples, blooms of the picoplankter *Aureococcus anophagefferens*, common for many years in the coastal lagoons of Long Island and Maryland, had severe negative effects on bay scallops, causing mass mortality and recruitment failure (Bricelj *et al.*, 1989), and also negatively affected growth of juvenile and adult hard clams (Greenfield and Lonsdale, 2002; Wazniak and Glibert, 2004). The small size, unpalatability, and/or nutritional quality of the brown tide species were thought to cause these adverse effects, rather than direct toxicity (but note that toxic activity of this species from a dopamine-like substance that inhibits feeding may also have been a factor; see Bricelj and Kuenstner, 1989; Draper *et al.*, 1990; Gainey and Shumway, 1991). Microzooplankton grazing was also reduced (Gobler *et al.*, 2002), and may have contributed to the prolonged maintenance of these blooms. Blooms of another picoplankter, *Synechococcus*, common in subtropical coastal lagoons like Florida Bay (Glibert *et al.*, 2004, 2010), also have been shown to negatively affect grazers. In this case, losses of filter feeders such as sponges may help prolong these blooms (e.g., Hall *et al.*, 1999; Philips *et al.*, 1999). The release of polysaccharides by *Synechococcus*, another physiological “overflow” metabolic pathway, is believed to obstruct the canal system of the sponges and thereby disrupt normal feeding (Sunda *et al.*, 2006, and references therein). Therefore, in a natural algal assemblage, some HAB species may be outcompeted by more rapidly growing species, but when grazers are disrupted and nutrient supply favors the HAB species, the probability of their success increases greatly. Thus, growth rate alone need not be the best “strategy” for bloom success; slowly growing HAB can become established and even dominant if their competitors or grazers are inhibited.

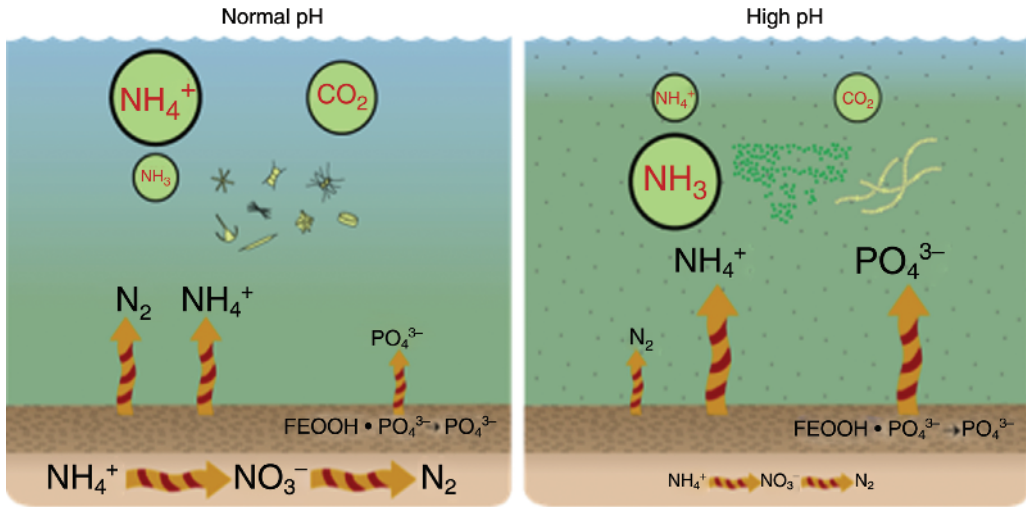
#### 1.4.3.2 Biogeochemical Alterations

Many HAB species, if able to establish and grow, can alter the chemical or biogeochemical environment in ways that may further sustain them. In highly productive, high-biomass systems, pH values vary substantially over diel periods or over the life span of a bloom. In highly productive freshwaters and estuaries, the pH trajectory is often one of increase, rather than the decrease that is the dominant direction of change occurring due to increased CO<sub>2</sub> and climate change; pH values > 9 commonly occur during dense blooms (Shapiro,

1997; Jacoby *et al.*, 2000; López-Archilla *et al.*, 2004; Glibert *et al.*, 2011; Gao *et al.*, 2012). Many HAB species are superior competitors under elevated pH, as many have highly effective C-concentrating mechanisms that allow them to sustain photosynthesis when other algae become C-limited or otherwise stressed from exposure to elevated pH (Jähnichen *et al.*, 2007; Glibert *et al.*, 2011, and references therein).

These dynamic pH swings create different challenges for organisms than do the acidification effects of acid deposition and climate change that affect oligotrophic waters (e.g., large oligotrophic lakes and pelagic ocean waters). Such elevated pH conditions may, in turn, alter bacterial metabolism and may also affect the biogeochemical cycling of N, including the chemistry of NH<sub>4</sub><sup>+</sup> and NH<sub>3</sub> and processes such as nitrification, denitrification, and dissimilatory NO<sub>3</sub><sup>-</sup> reduction to NH<sub>4</sub><sup>+</sup> (DNRA), as well as the efflux of P from the sediment (Seitzinger, 1991; Kemp *et al.*, 2005; Tank *et al.*, 2009; Gao *et al.*, 2012; Figure 1.5). As the pH increases, fundamental physical-chemical relationships related to P adsorption and desorption change, leading to enhanced release of this important nutrient (Jordan *et al.*, 2008; Glibert *et al.*, 2011, 5). Enhancement of sediment P release under elevated water-column pH conditions has been observed in eutrophic lakes and estuaries (Andersen, 1974; Drake and Heaney, 1987; Jensen and Andersen, 1992; Xie *et al.*, 2003) and tidal freshwater/oligohaline estuaries, and the success of the cyanobacterium *Microcystis* in high-biomass blooms has been attributed to that effect (Seitzinger, 1991; Glibert *et al.*, 2011; Gao *et al.*, 2012). While P may not be available in the water column in concentrations that would be considered sufficient to sustain these blooms, the rate of recycling from the benthos can supply the required P and/or N. Efflux of NH<sub>4</sub><sup>+</sup> also increases under elevated pH. The elevated pH conditions that are created under high-biomass blooms may be unfavorable for many algal species, but not necessarily for the HAB species.

MacIntyre *et al.* (2004) suggested another biogeochemical feedback pathway that may contribute to some HAB, wherein the accumulation of biomass and the concomitant reduction in light attention lead to loss of productivity at the benthos due to light shading. If benthic microalgae decrease, competition for nutrients at the sediment surface is reduced, favoring the water-column species. Loss of benthic primary producers may also increase the rate of flux of nutrients from the sediments because the benthic microalgae are



**Figure 1.5** Conceptual diagram of the effect of altered pH and altered salinity on the processes of exchange of  $\text{PO}_4^{3-}$  and  $\text{NH}_4^+$  from the sediment to the water column. With a rise in pH, or a shift to higher salinity, the sediment flux of  $\text{NH}_4^+$  and  $\text{PO}_4^{3-}$  increases via the mechanisms described in text. The pH also alters the equilibrium between  $\text{NH}_4^+$  and  $\text{NH}_3$ , leading to higher  $\text{NH}_3$  at high pH. *Source:* Reproduced from Glibert *et al.* (2011) with permission of Taylor & Francis.

no longer present to “intercept” these nutrients at the sediment–water interface (*sensu* Carlton and Wetzel, 1988). Also, loss of benthic algae can destabilize the cohesion of sediments, allowing for increased nutrient flux and resuspension under wind events (MacIntyre *et al.*, 2004; Sunda *et al.*, 2006). These examples are just a few of the types of feedbacks that can help to sustain a system in a condition suitable for HAB species once they have become established.

#### 1.4.4 Climate Change

Climate controls many of the fundamental parameters regulating algal growth, including water temperature, nutrients, light, and grazers, and thus can be expected to influence changes in the species composition, trophic structure, and function of aquatic ecosystems. Global temperatures are on the rise, a fact now well accepted to be related to anthropogenic activities (Intergovernmental Panel on Climate Change [IPCC], 2007, 2014). Average sea surface temperatures are expected to rise as much as 5 °C over the coming century, leading to a freshening of many oceanic regions due to ice melt and altered precipitation (e.g., Moore *et al.*, 2008; Doney, 2010; Fu *et al.*, 2012b, and references therein). These changes, in turn, will alter stratification, availability of nutrients and their forms and ratios,  $\text{pCO}_2$ , and light regimes, and grazing activity among other factors (e.g., Boyd and Doney,

2003), all of which control the extent to which HAB become established, recurrent features.

Temperature affects growth rate, motility, germination, pigment content, enzyme reactions, photosynthesis, and various other processes, affecting the ability of cells to thrive in a particular area (e.g., Wells *et al.*, 2016, and references therein). Increasing temperatures positively affect taxa with higher temperature optima for growth, and negatively influence taxa that have lower temperature optima. Negative influences of increasing temperature disproportionately affect diatoms, as they generally thrive in colder seasons, and tend to have colder temperature optima than other microalgal groups (Harris, 1986; Graham *et al.*, 2016, and references therein). Moreover, rates of uptake of  $\text{NO}_3^-$  and of its reduction to  $\text{NH}_3$  generally decrease at higher temperatures, especially above 15–18 °C (e.g., Lomas and Glibert, 1999a; Glibert *et al.*, 2016), further suggesting that diatoms are negatively affected as temperatures rise. In contrast, many cyanobacteria and dinoflagellate species, including HAB species, prefer warmer temperatures (e.g., Paerl and Huisman, 2008; Paerl and Scott, 2010). Temperatures also affect the consortium of organisms that co-occur with the harmful algal species, including bacteria, viruses, competing phytoplankton taxa, and grazers (Wells *et al.*, 2016, and references therein). Toxicity of many harmful algal species also increases with warming (Davis *et al.*, 2009; Fu

*et al.*, 2012, and references therein). The combination of elevated  $p\text{CO}_2$  together with nutrient limitation and altered nutrient ratios appears to be especially potent in affecting the toxicity of some harmful algal species. On the other hand, for some species, higher toxicity associated with warming may promote slower growth rates (e.g., Ogata *et al.*, 1989; Lewis *et al.*, 1993), but, as noted in this chapter, slower growth rates need not be detrimental to HAB formation.

Examples can be found through the United States and European coasts where long-term data are available, showing positive correlations between increasing mean water temperature and shifts in HAB species and the timing of their outbreaks. Warmer temperatures can contribute to range expansion of particular species. Higher temperatures promote increased water-column stability and increased thermal stratification which, in turn, favor known bloom-forming, toxigenic cyanobacterial species that control their vertical position through internal buoyancy regulation (e.g., Walsby, 1975; Visser *et al.*, 2016, and references therein). Under higher vertical mixing, diatoms are superior competitors; thus, as stratification increases, diatoms are more apt to sink out of the water column (Visser *et al.*, 2016, and references therein). Moreover, at higher temperatures water can become less viscous, buoyant cyanobacteria can change their vertical position more rapidly, and sinking diatoms sink faster (e.g., O'Neil *et al.*, 2012, and references therein). Thus, with climate change, diatoms may be negatively affected in several ways.

As mentioned, warming trends are causing changes in the C cycle, resulting in acidification of the oceans and some estuaries, an effect on pH opposite that due to high biomass blooms and their drawdown of  $\text{CO}_2$ . As pH declines, there is some evidence that some cyanobacteria can increase growth rates and therefore outcompete eukaryotic algae under such conditions (O'Neil *et al.*, 2012, and references therein). Flynn *et al.* (2015), in a series of experiments coupled with modeling approaches, illustrated the complexity of effects of ocean acidification coupled with eutrophication (and oligotrophication) on phytoplankton species succession. They reported a potential for altered primary production, depending on local conditions and bloom composition. Their work also suggested that, when coupled with effects on grazers, ocean acidification and eutrophication will increase the frequency of HAB, including blooms of mixotrophic species.

The interacting effects of  $p\text{CO}_2$ , temperature, and nutrient supply complicate the interpretation

of effects of  $p\text{CO}_2$  on HAB toxicity (e.g., Boyd and Hutchins, 2012; Gobler *et al.*, 2016). High  $\text{CO}_2$  may also affect toxicity of HAB through various routes. An overall trend of increasing toxicity with increasing  $p\text{CO}_2$  has been reported for numerous strains of cultured *Alexandrium ostenfeldii* (Kremp *et al.*, 2012), but culturing approaches can affect the extent to which relationships are observed between elevated  $p\text{CO}_2$  and toxicity in some harmful algal species (Van de Waal *et al.*, 2011). The synthesis of at least some toxins is light dependent, as for karlotoxin production by *Karlodinium veneficum* and saxitoxin production by *Alexandrium catenella* (Proctor *et al.*, 1975; Adolf *et al.*, 2008), suggesting that as photosynthesis is affected by changing  $p\text{CO}_2$ , toxin synthesis is also altered. Species that produce copious amounts of reactive oxygen species (ROS), such as raphidophytes (Raphidophyceae), also produce more ROS under high light conditions (Fu *et al.*, 2012b, and references therein). In the toxigenic diatoms *Pseudo-nitzschia multiseries* and *P. fraudulenta*, concentrations of their toxin, domoic acid, have been shown to increase at high  $\text{CO}_2$ /low pH (e.g., Sun *et al.*, 2011; Tatters *et al.*, 2012). This effect has been more pronounced when cells were nutrient-limited, or when forms of N shifted from oxidized to reduced forms (Glibert *et al.*, 2016, and references therein).

Climate change may further influence harmful algal species expansions due to altered precipitation patterns, including increases in droughts in some regions and increased frequency or intensity of storm events in others. Episodic storm events and climate variability affect the timing of freshwater flow, water residence times, the magnitude and timing of nutrient pulses, and resulting biotic responses; in other words, these factors affect the magnitude and timing of how nutrients “get there” (e.g., Miller *et al.*, 2006; Burkholder *et al.*, 2006; Mallin and Corbett, 2006; Paerl *et al.*, 2006; Heisler *et al.*, 2008). As examples, within days after Hurricane Isabel in 2003, a large phytoplankton bloom developed in Chesapeake Bay, linked to increased nutrient loads (Miller *et al.*, 2005). Algal blooms and extensive hypoxia/anoxia occurred shortly after several hurricanes affected the lagoonal Neuse River Estuary in the 1990s (Burkholder *et al.*, 2004, 2006). A bloom of the picocyanobacterium *Synechococcus* in eastern Florida Bay, lasting more than 18 months, followed an injection of nutrients from the high freshwater discharge caused by Hurricanes Katrina, Rita, and Wilma in 2005 (Glibert *et al.*, 2009). Also in Florida, releases of Lake Okeechobee water to the lagoons

along the northeast were accelerated in 2016 due to heavy rains, and the nutrient pollution carried with these flows resulted in what was termed a “guacamole-thick” bloom of cyanobacteria, mostly *Microcystis* (Mettler, 2016).

In coastal lagoons, where riverine input is not the dominant source of nutrient delivery, climate variability can alter the input of groundwater nutrients (e.g., LaRoche *et al.*, 1997). Long-term changes in, or intensification of, climate forces such as monsoons or interannual oscillations, such as those related to the El Niño Southern Oscillation (ENSO), or longer term cycles, such as the North Atlantic Oscillation (NAO) and Pacific Decadal Oscillation (PDO), can also alter conditions for HAB species. In the northern Iberian Peninsula, for example, the harmful dinoflagellate *G. catenatum* was abundant during the mid-1980s when there was a transition from downwelling-favorable conditions to upwelling-favorable conditions, following a shift in the NAO index (Alvarez-Salgado *et al.*, 2003). In late 2013, and continuing through much of 2016, anomalously warm water developed in the northeastern Pacific Ocean (e.g., Bond *et al.*, 2015; Freeland and Whitney, 2015), a feature associated with the unusually strong El Niño event and the PDO. The warm water moved over the continental margin, eventually extending from southern California to Alaska by spring 2015. Coupled with seasonal upwelling, conditions were ideal for *Pseudo-nitzschia* that had sufficient nutrients, and the right nutrient forms, to proliferate and suitable temperatures for rapid growth. Regulatory limits of domoic acid were exceeded along the entire coast for months, and toxin impacts were sustained at many levels of the food web, from razor clams and Dungeness crabs to sea lions and whales and porpoises (McCabe *et al.*, 2016). This was the largest toxic *Pseudo-nitzschia* bloom on the West Coast thus far, and portends of future outbreaks with conditions of increasing temperature and nutrient supply. Collectively, the intersection of nutrient loading with changes in precipitation patterns, temperature, and CO<sub>2</sub> patterns alters the trajectory of both cells and nutrients to “get there,” and the resulting environmental conditions make it more conducive for the harmful algae to “be there.”

## 1.5 Conclusions

This review has emphasized that the success of harmful algal species, and therefore the cause of blooms, lies at the intersection of environmental

conditions, particularly nutrient conditions, physiological adaptations of the harmful species (or strain), interactions with co-occurring organisms (trophodynamically and biogeochemically), and physical dynamics that can serve to aggregate or disperse cells or their nutrients. There is ample evidence to conclude that the global expansion of HAB, both marine and freshwater, is due to anthropogenic changes. The anthropogenic footprint is not, however, limited to nutrient pollution. Anthropogenic activities have affected trophodynamics from both overfishing and intensive aquaculture, hydrodynamics of major river systems and flow due to dam construction and increasing consumptive water demands, and climate.

In all, there is overwhelming evidence that both species introductions and nutrient loads are changing regionally and globally; they “get there” and are “getting there” more often, through many sources and pathways. Much has been learned about the physiological adaptations of many phytoplankton, both HAB and non-HAB species, including their differing optimal N:P ratios; their preferences for, or tolerance of, different nutrient forms; and pathways of “overflow metabolism” under conditions of excess nutrients. They have good physiological reasons for “being there.” Physical dynamics that lead to retentive zones or favorable hydrographic conditions, including anthropogenically altered flow dynamics, help cells “stay there.” Changes in climate and other reinforcing feedbacks, through trophodynamic and biogeochemical changes, also contribute to HAB “staying there” when they occur. Warming temperatures, precipitation changes, changes in water-column acidification due to changes in atmospheric CO<sub>2</sub>, and alteration of the C system due to excessive productivity (basification from dense bloom formation), coupled with changes in water-column stability, are creating many “windows of opportunity” for HAB to thrive. More blooms are occurring in more places, more often, and lasting longer. There are, of course, various examples where blooms have occurred uncoupled to anthropogenic changes. Nevertheless, production of new biomass requires nutrients. Therefore, for HAB blooms that develop high biomass above what is naturally supported, an exogenous nutrient supply must have been provided. Anthropogenic nutrient pollution is a common source of these exogenous nutrients. Warmer, more stable water columns help to accelerate the change in habitat suitability.

There are many opportunities to advance understanding of HAB and environmental changes. Such

advances need to be achieved across the full spectrum of scales, from the dynamic regulation of genes and physiology of different function groups and species, to the land-, sea-, and air-scape changes that are occurring due to the vast array of global changes, and the feedbacks between biogeochemistry and trophodynamics (Glibert *et al.*, 2013; Kana and Glibert, 2016). There is an urgent need to advance our conceptual understanding of nutrient regulation of algal assemblages beyond the classic focus on nutrient limitation. Compositional changes in algal assemblages occur when nutrients change in proportion or form, at all concentration levels, from limiting to super-saturating. Recognition of the vast anthropogenic effects that nutrient pollution, harvesting and production of food (including associated fertilizer use), and altered hydrodynamics for water consumption or electricity generation are having on the globe is fundamental to understanding how these changes affect ecological function and biodiversity, including microbial biodiversity.

The many challenges of an increasingly nutrient-enriched, HAB-impacted globe should be cause to motivate the development of a new suite of dynamically and stoichiometrically complex models, and new experimental investigations to provide the requisite data to parameterize them so that they are reliably predictive. The major management implication is clear: the most effective actions to reduce HAB and their impacts will be continued efforts to reduce nutrients. New management approaches that focus on dual nutrient (N and P) control and regulation of nutrient forms, beyond simply TN and TP, will be required for effective management of HAB. It must be emphasized that singular nutrient reductions, which characterized many management efforts in the past, can exacerbate the widespread imbalances in nutrient ratios. The challenges of controlling nutrients and managing HAB (getting there, being there, and staying there) will continue to be great.

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