

THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

CITATION

Glibert, P.M., and M.A. Burford. 2017. Globally changing nutrient loads and harmful algal blooms: Recent advances, new paradigms, and continuing challenges. *Oceanography* 30(1):58–69, <https://doi.org/10.5670/oceanog.2017.110>.

DOI

<https://doi.org/10.5670/oceanog.2017.110>

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Globally Changing Nutrient Loads and Harmful Algal Blooms

Recent Advances, New Paradigms, and Continuing Challenges

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Many HABs produce vividly colored blooms of cells that accumulate in surface waters. These high biomass blooms can cause hypoxia, can contribute to the toxicity of fish and shellfish, and can cause other environmental problems. (background) Bloom of a “red tide” caused by the species *Noctiluca* off the famous Bondi Beach in Sydney, Australia. Photo credit: <http://wayoutfar.com/red-algae-closes-our-favourite-sydney-beach-bondi>

ABSTRACT. It is now well recognized that there are more harmful algal blooms (HABs), more often, in new and different places, often lasting longer, and with a range of toxicities, and that many of these blooms are related to nutrient pollution. Nutrient loads are increasing globally, but they are changing regionally in proportion and in the dominant form of nutrient. The fact that nutrient loads have generally increased is, in itself, insufficient for the promotion of HABs. The success of HABs lies at the intersection of the physiological adaptations of the harmful algal species, environmental conditions, and interactions with co-occurring organisms that alter abiotic conditions and/or aggregate or disperse cells, in turn promoting or inhibiting their growth. It is a change in the supply of the right nutrients at the right time that helps to create conditions conducive to specific HABs. Many dinoflagellate and cyanobacterial HABs appear to have adaptations that allow them to exploit environments—and potentially even become more toxic—where nutrients are not in balanced (Redfield) proportions. HABs are also changing in complex ways due to changes in climate and many other changes that affect the timing, amount, or proportions of nutrients. There is much work to be done to understand the physiological ecology of HABs and other co-occurring species. Climate change and altered CO₂ levels, and their implications for altered productivity of the global ocean, should motivate both new models and new experimental investigations that support them. Based on current knowledge, the management implications are clear: the most effective actions to reduce HABs and their impacts will be continued efforts to reduce nutrients entering our waters.



INTRODUCTION

Not much more than a decade ago, there was considerable debate about whether harmful algal blooms (HABs) were increasing globally, and if they were, whether such an increase was related to changes in the environmental availability of nutrients. While some lingering skeptics remain, and indeed there are blooms that are unrelated to nutrient pollution, by and large, debate has ceased. We now recognize that there are more blooms, more often, in new and different places, often lasting longer, and with a range of toxicities, and that many of these blooms are related to the global increase in nutrient pollution. Relationships between nutrients and HABs have become nearly synonymous with eutrophication, and large-scale blooms that visibly discolor water are often in the public eye (see photo on opposite page).

While nutrient pollution is the primary driver of eutrophication, we now recognize that the relationship between nutrient pollution and HABs is more complex than previously thought (Glibert et al., 2005; Heisler et al., 2008): not all nutrient loads result in HABs, and not all nutrient effects that result in HABs cause other eutrophication impacts (i.e., visible scums, hypoxia). Nutrient inputs yield changes in HAB biomass, but the how and why of changes in biodiversity are far more complicated. The success of HABs lies at the intersection of the physiological adaptations of the harmful algal species and/or strain (population), the environmental conditions, and interactions with co-occurring organisms (both biogeochemically and trophodynamically) 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 (Glibert and Burkholder, in press). Substantial advances have been made over the past decade in unraveling all of these interactions.

“Eutrophication” has been defined in various ways (e.g., Nixon, 1995; Richardson and Jørgensen, 1996). Central

to all definitions is the concept that the enrichment of water by nutrients accelerates the growth of algae and higher forms of plant life, which leads to an undesirable disturbance in the balance of organisms present in the water and alters the quality of the water concerned. The result of eutrophication is often an increase in total algal biomass, frequently dominated by one or more species or groups. Such blooms may have deleterious effects, including overgrowth and shading of seaweed and seagrass, oxygen depletion of the water from algal respiration or decay of algal biomass, direct toxic effects on fish and shellfish, suffocation of fish from stimulation of gill mucus production, and mechanical interference with filter feeding by fish and bivalve molluscs. Deleterious effects on other benthic species may also be considerable. Of additional concern with the development of high-biomass algal blooms is the poor transfer of energy to higher trophic levels, as many bloom species are not efficiently grazed, resulting in decreased transfer of carbon and other nutrients to fish stocks when they replace desirable algal species.

Much of our improved understanding of the relationships between nutrient loads and changes in biodiversity comes from advancement away from what Cloern (2001) described as a “phase 1” model of eutrophication—the perception that more nutrients fuel more biomass through direct dose-response relationships. While such a limited perspective is appropriate in consideration of high biomass blooms that depend on large injections of new nutrients, it is now understood that nutrient loads are complicated in terms of overall amounts, proportions, and timing, and responses to them are complicated in terms of changes in biodiversity (including HABs), food web interactions, and biogeochemical changes. Ecosystem changes associated with nutrient enrichment are also occurring in concert with many other ecosystem changes, not the least of which are related to alterations in climate.

This article highlights some of the

research conducted on HABs and eutrophication in the decade since Glibert et al. (2005) published on this topic in *Oceanography*. This paper builds on key contributions undertaken under the umbrella of the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) program, along with other allied efforts. We particularly highlight key advances in physiology and modeling at all scales that have helped to advance understanding of the complexity of the nutrient-HAB relationship. Thus, this paper follows the structure of the 2005 *Oceanography* synthesis on HABs and eutrophication, highlighting advances and challenges (Glibert et al., 2005). However, it is not our intention to synthesize knowledge on the vast numbers of species that have increased in concert with nutrient pollution; such syntheses can be found throughout the literature. This contribution ends with some suggestions on research priorities for the next decade.

THE INSATIABLE APPETITE FOR N AND P—THE GLOBAL VIEW

Many reports and papers review the increase in nutrient pollution due to the increase in human population, rising demands for energy, increases in nitrogen (N) and phosphorus (P) fertilizer use for agriculture, changes in human diet leading to more meat production and animal waste, and expanding aquaculture industries (e.g., Smil, 2001; Galloway and Cowling, 2002; Howarth et al., 2002; Glibert et al., 2006). The sources of nutrients from land, air, and even water continue to change. The acceleration in the use of N fertilizers, catalyzed by the development of industrial capability to convert N₂ gas in air into fertilizer (the Haber Bosch Process), has contributed to the “green revolution” responsible for increased food production that has supported the expansion of human population from ~2 billion in the early twentieth century to >7 billion people today (Smil, 2001; Erismann et al., 2008). Global use of N fertilizer has increased ninefold, while that of P has increased threefold

in the past four decades (Sutton et al., 2013; Glibert et al., 2014b; Figure 1). In fact, 85% of all synthetic N fertilizers have been created since 1985 (Howarth, 2008).

Agricultural crops only take up 50% of the N fertilizer applied (Peoples et al., 1995). The remainder is lost via various pathways, including ammonia volatilization, denitrification, runoff, and leaching, or it is accumulated in the soil. Animal agriculture is expanding to meet the dietary demands of a growing population, and increasingly, animal production is concentrated in large industrial feeding operations. Animal waste can be a major source of nutrient pollution. Moreover, nutrient inputs from culture of finfish, shellfish, and macroinvertebrates are a growing concern as the importance of aquaculture in providing fish food supplies continues to escalate. Animal waste and excess animal feed contribute to the “leaked” nutrients that ultimately enrich our lakes, rivers, and coastal waters. Collectively, these

changes in nutrient sources and loads are thought to be affecting biodiversity from land to sea, beginning at the level of the N content at the genome and proteome level (Acquisti et al., 2009; Peñuelas et al., 2012). Emphasis is placed on N because, in contrast to the enormous expansion in the global use of chemical N fertilizers, use of P fertilizers has shown a much smaller increase, at a rate only about one-third that of N (Sutton et al., 2013; Glibert et al., 2014b). The fact that nutrient loads have generally increased is, in itself, insufficient for the promotion of HABs. It is a *change* in nutrient loads that leads to the supply of the right nutrients at the right time to help create conditions conducive to specific HABs. Altered nutrient supply can be a function of increased nutrient pollution on the one hand, but also may be a result of factors that result in reduction of one nutrient relative to another. Thus, aggressive removal of single nutrient sources, such as P loads from sewage effluent and laundry detergents, is also

accelerating this change (e.g., Litke, 1999). HABs result when there is an intersection of the right growth conditions and physiological adaptation by individual species that can exploit those conditions.

PHYSIOLOGICAL DIVERSITY IN NUTRIENT STRATEGIES

Resource ratio theory (Tilman, 1977; Smayda, 1990) predicts that as the ratios of different essential elements change, the community structure will change due to competition between algae with different optimal nutrient ratios. The “optimum” N:P is when 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. Given that phytoplankton span many orders of magnitude in cell volume, from $<2 \mu\text{m}$ to more than $4,000 \mu\text{m}$, it should not be surprising that different types of phytoplankton have different elemental demands (Finkel et al., 2010, and references therein).

Many dinoflagellate and cyanobacterial HABs appear to have adaptations that allow them to exploit environments where nutrients are not in Redfield proportions. Not all HABs, or even all species within HAB groups, necessarily have such adaptive strategies (Glibert and Burkholder, 2011), but those that do will have advantages for growth. Among the strategies for success in environments with comparatively low P relative to N availability is to have a lower cellular requirement than competitor species. Very small cells, such as picocyanobacteria, have a lower requirement for P due to their reduced need for structural components in the cell (Finkel et al., 2010). Another strategy is the ability to “make do with less,” which may be accomplished by physiological substitution of a P-containing lipid with a non-P-containing lipid (sulfolipid), and many cyanobacteria are able to do this (Van Mooy et al., 2009). A third strategy is the ability to acquire P in organic or particulate form via a range of enzymes that

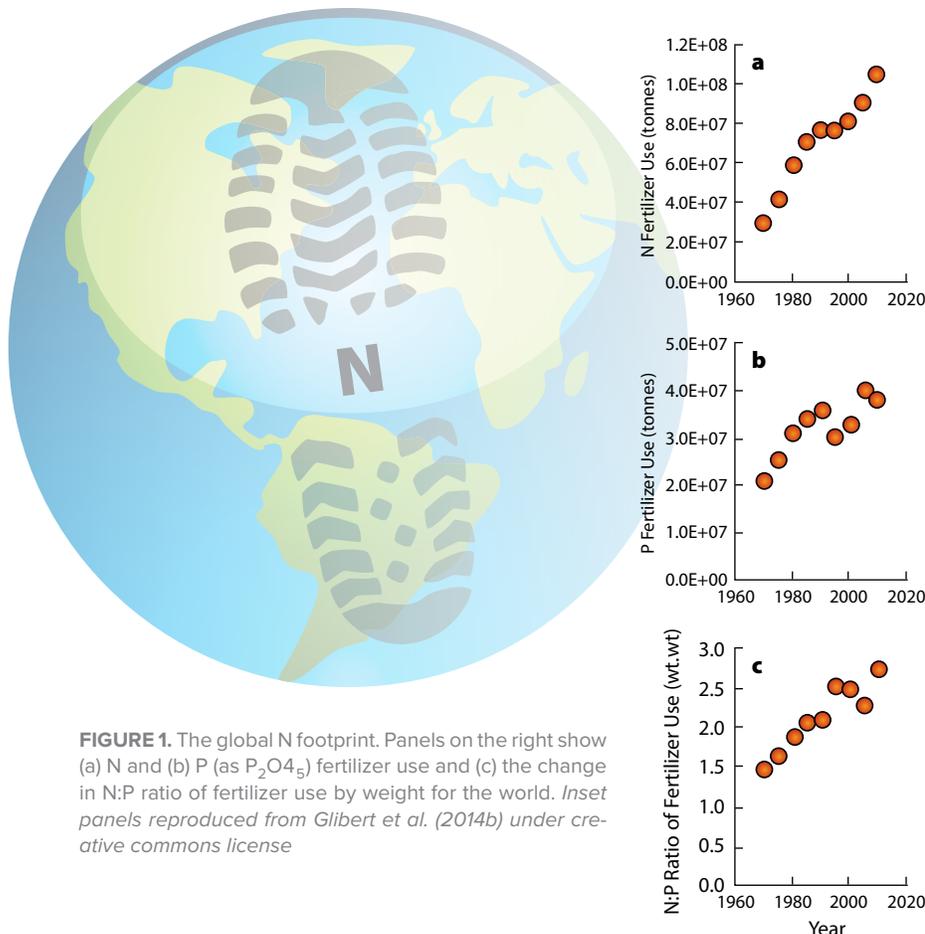


FIGURE 1. The global N footprint. Panels on the right show (a) N and (b) P (as P_2O_4) fertilizer use and (c) the change in N:P ratio of fertilizer use by weight for the world. Inset panels reproduced from Glibert et al. (2014b) under creative commons license

convert organic to inorganic forms, or to mixotrophy, the ability to ingest particulate nutrients. These strategies may provide some cells with a source of P not available to those cells dependent on inorganic P for their nutrition. Mechanisms for accessing limited P supplies include the upregulation of genes associated with high affinity, phosphate-binding proteins, and alkaline phosphatase (Harke et al., 2012). Fewer species have been shown to hydrolyze the more refractory phosphonates, and it has been proposed that this ability gives them a competitive advantage over other species in low P environments (e.g., Illikchyan et al., 2009). There are also differences in cell storage between N and P: when P supplies are limited, P may simply be stored within cells to allow growth for extended periods (e.g., Burford et al., 2014; Willis et al., 2015). These strategies help to promote groups such as cyanobacteria and many HAB dinoflagellates when N is supplied far in excess of P.

Considerable emerging evidence indicates that nutrient proportions affect toxin production as well. Many cyanobacteria and marine dinoflagellate HABs are more toxic when N is in stoichiometric excess over P. The evidence for toxin production increasing under non-stoichiometrically balanced conditions is considerable (e.g., Granéli and Flynn, 2006; Hardison et al., 2012, 2013). Most notably, excess N over P availability has been related to the production of microcystin (MC), the toxin of the freshwater cyanobacterium *Microcystis* among other species, under controlled chemostat conditions and in natural populations (Van de Waal et al., 2009, 2010; Monchamp et al., 2014; Harris et al., 2016). As recently reviewed by Gobler et al. (2016), common cyanotoxins, including MC, nodularins, cylindrospermopsins, and saxitoxins, have amino acid precursors, either glutamine, arginine, or leucine, and they, in turn, depend on adequate N supply for their assimilation. In the dinoflagellate *Alexandrium tamarense*, saxitoxin production has been shown to increase by three- to fourfold under P deficiency

(reviewed by Granéli and Flynn, 2006). Additionally, a study of the dinoflagellate *Karenia* found that P-limited cells had a higher cellular toxin quota than P-replete cells (Hardison et al., 2013). Furthermore, 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 was shown to increase in the diatom *Pseudo-nitzschia multiseriis*. There are also examples of toxin production being stimulated at the opposite N:P spectrum. The proportion of toxic strains of the freshwater cyanobacterium *Cylindrospermopsis raciborskii* increased when P was added to mesocosms (Burford et al., 2014), and the haptophyte *P. parvum* is also more toxic under low N:P (as well as high N:P) compared to balanced nutrient conditions (Granéli and Flynn, 2006). 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).

LIKES AND DISLIKES: NUTRITIONAL PREFERENCES

In addition to nutrient ratios that promote species with higher or lower requirements for particular nutrients, the form in which a nutrient is supplied may also control whether a specific nutrient load will promote a HAB. Experimental evidence supports the notion that diatoms are specialists in the use of oxidized forms of N (such as NO_3^-), while cyanobacteria, including freshwater cyanobacteria and dinoflagellates, are specialists in reduced forms of N (such as NH_4^+ , urea, or organic N). Recent reviews of the physiological bases of N uptake, as well as molecular and meta-transcriptomic data, lend considerable support to this emerging conclusion (Wilhelm et al., 2006; Glibert et al., 2016). Such differences are consistent with there being separate evolutionary lineages of these species, based

on increased understanding of the physiology of these different functional groups.

A number of examples illustrate these patterns, a few of which are highlighted here. The brown tide organism *Aureococcus anophagefferens* has been shown to prefer organic N over NO_3^- (Berg et al., 1997). Recent ecogenomic studies reveal that the ability of *A. anophagefferens* to outcompete co-occurring phytoplankton where dissolved organic matter and turbidity are high, and dissolved inorganic N concentrations are low, may be a result of its larger number of genes involved in light harvesting, organic carbon and N use, and trace metal utilization compared with competing phytoplankton (Gobler et al., 2011). Studies in freshwater systems also show different responses of individual species within mixed populations to different forms of N, including urea (Donald et al., 2011, 2013). Additionally, Finlay et al. (2010) showed that non-heterocystic cyanobacteria dominated over heterocystic cyanobacteria when urea was added to mesocosms in lakes. Many other studies have also shown organic use by HABs (e.g., Cochlan et al., 2008; Heisler et al., 2008, and references therein)

There is also evidence that the form of N affects toxin production. 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 (dissolved organic nitrogen and NH_4^+ ; Monchamp et al., 2014). Furthermore, in mesocosm studies, additions of NH_4^+ led to higher MC concentrations and cyanobacterial blooms of longer duration compared with experiments in which NO_3^- was the added N substrate (Donald et al., 2011). A recent study by Harris et al. (2016) extended our understanding of N forms and toxins. They documented for midwestern US reservoirs that elevated ratios of $\text{NH}_4^+:\text{NO}_3^-$ provided conditions that favored the production of secondary metabolites of cyanobacteria, among which were

Microcystis toxins. The metabolites MC, geosmin, and 2-methylisoborneol were all favored under elevated $\text{NH}_4^+:\text{NO}_3^-$ ratios. Laboratory studies also show toxin cellular content to be higher for dinoflagellate *Alexandrium tamarense* cells grown on NH_4^+ and urea rather than on NO_3^- (Leong et al., 2004). Armstrong-Howard et al. (2007) found that natural assemblages of *Pseudo-nitzschia* (dominated by *P. australis*) can potentially double their toxin production when growing on urea-N compared to growth on either NO_3^- or NH_4^+ , and that in a *Pseudo-nitzschia australis*-dominated bloom, urea comprised 17% of the ambient N substrates.

EAT, DRINK, AND BE MERRY: THE SUCCESSFUL MIXOTROPHS

An important advancement in the understanding of HABs and their nutrition over the past decade or so has been 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). Our understanding of mixotrophy fundamentally changes our understanding of planktonic food webs. It was once thought that organisms that could combine phototrophy and phagotrophy were just curiosities, but now it is recognized that the bulk of the base of this food web is supported by protist plankton communities that are mixotrophic (Flynn et al., 2013; Mitra et al., 2014). As Mitra et al. (2014, p. 996) argued, purely phototrophic organisms are likely to be dominant only during the developmental stages of an ecosystem (i.e., during spring blooms or in early upwelled waters) but, “as these waters and their ecosystems mature, their nutrient conditions and particulate organic loading change, giving rise to conditions that favor

mixotrophy. Therefore, during much of the planktonic production cycle these mixotrophs are abundant if not dominant.” (See Figure 2.)

Mixotrophy allows HABs to acquire nutrients in pre-packaged or particulate form, especially when sufficient dissolved nutrients are not available in the environment or when nutrients are available but in imbalanced proportions, as is frequently the case in eutrophic waters (Burkholder et al., 2008; 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 source when there is an elemental imbalance in dissolved (water-column) nutrient substrates (e.g., Granéli et al., 1999; Stoecker et al., 2006). Recent laboratory experiments also show that at least for some mixotrophs, grazing is highly dependent not only on their physiological or nutritional state but also on that of their prey (e.g., Lundgren et al., 2016; Lin et al., in press). Mixotrophy may also be of particular importance in the maintenance of blooms, allowing them to be sustained for longer periods than would be the case if the cells depended only on dissolved nutrient availability (e.g., Glibert et al., 2009).

Most harmful dinoflagellates, haptophytes, and raphidophytes are mixotrophs to some degree, and many of them feed on their autotrophic competitors or become prey for other mixotrophs (e.g., Jeong et al., 2010). In some instances, toxins are used to capture prey and, thus, are directly related to the mixotrophic capacity of the organisms (Granéli and Flynn, 2006; Stoecker et al., 2006; Adolf et al., 2007). The dynamic interactions between mixotroph nutrition and toxin production may also be related to cell stoichiometric (im)balance, perhaps associated with the provision of secondary metabolites from photosynthetic pathways (Glibert and Burkholder, 2011). Furthermore, toxin production and mixotrophy are synergistic: release of toxins harms prey by releasing dissolved nutrients or making the prey easier to capture, which, in turn, can enhance growth rates.

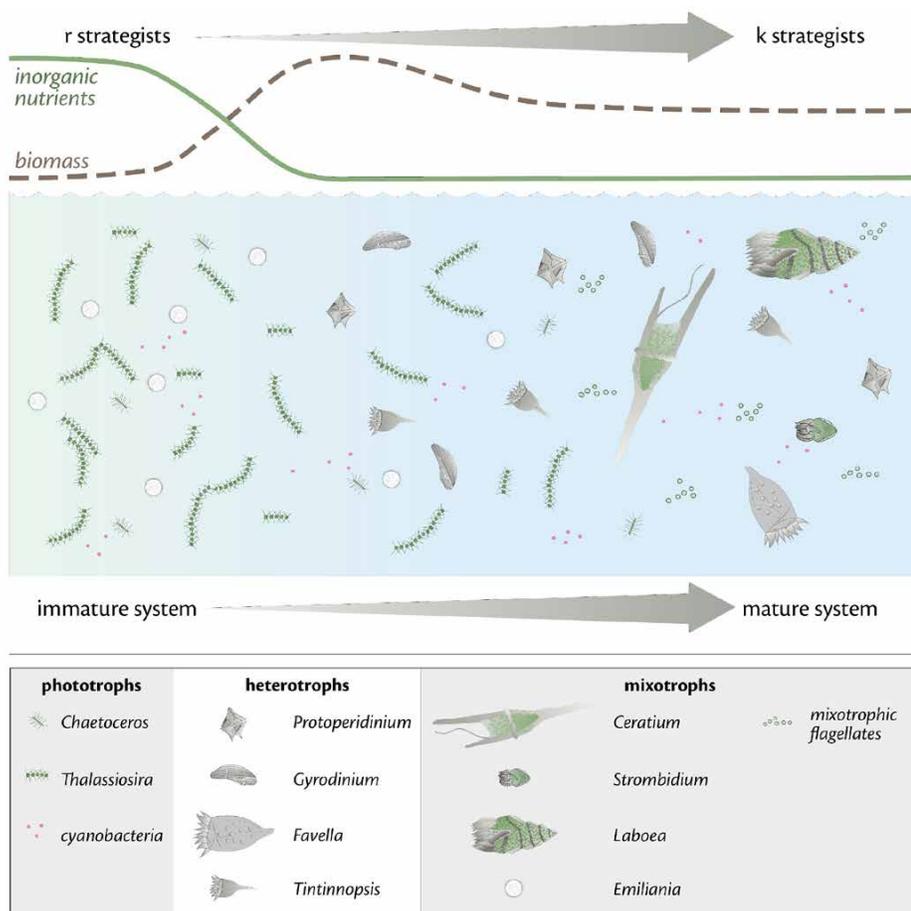


FIGURE 2. Transitions of an ecosystem with changing dominance from phototrophy to mixotrophy as inorganic nutrients are consumed. Figure reproduced from Mitra et al. (2014) under creative commons license

EMERGING ORDER FROM COMPLEXITY

As noted by Babin et al. (2005, p. 225) in their discussion in *Oceanography* of new approaches and technologies for observing HABs, “Integration is the answer: molecular biology and bio-optics with ocean observation technology; physiological ecology with oceanography and numerical modeling; real-time observing systems with ongoing efforts in monitoring and research.” Understanding and quantifying the relationships between eutrophication and HABs, and developing both short- and long-term predictive capabilities, requires a suite of modeling approaches, from conceptual to mechanistic, and parameterizing such models demands a new suite of experiments and data. Several authors have argued for the need for a new generation of plankton models based on emerging knowledge of dynamic cellular and ecophysiological behavior (e.g., Allen and Polimene, 2011; Flynn, 2010; Glibert et al., 2013). Natural resource managers and public health officials need better tools to forecast HAB events and to predict the composition of algal species, assemblages, and toxins that may occur under conditions of changing nutrient loads. There is a need for well-parameterized physiological models and improved conceptual, mechanistic, and integrated ecosystem models. Conceptually, these needs can be viewed as components of a nested suite of models.

The most well-recognized and cited conceptual model of HAB formation is the Margalef “mandala,” a diagram elegant in its simplicity, yet rich in insight (Margalef, 1978; Margalef et al., 1979). It captures the essence of much of the importance of the balance between physical forces and nutritional forces (Figure 3), highlighting the distinction in distribution of organisms that thrive under turbulent, nutrient-rich conditions (diatoms), and those that tend to thrive under more nutrient-poor, low-turbulence environments (dinoflagellates). There have been many efforts to improve on this conceptual model. The

most recent emphasizes the need to differentiate the effects of N and P loadings, as well as differences in N form (Glibert, 2016). It places these differences in conceptual space against other environmental characteristics, including adaptation to high versus low light and the tendency to be autotrophic versus mixotrophic, cell motility, environmental turbulence, pigmentation quality, temperature growth preference, cell size, relative growth rate, relative production of bioactive compounds such as toxins or reactive oxygen species (ROS), r versus K strategy (see Parry, 1981), and fate of production in terms of grazing. The revised mandala (Figure 4) highlights the differences and trade-offs between traits and/or environmental conditions, and illustrates that some traits tend to track each other, a concept that may be helpful in trait-based modeling approaches. Such a conceptual model is instructive in that with a focus only on factors related to nutritional or growth physiology, the major phytoplankton functional groups are, in fact, differentiated. But, an important lesson can be learned from the tradition of mandala making: while the balance and interaction of the universe is fascinating, it is also in flux. Monks often destroy their intricately beautiful mandalas once completed, underscoring that nothing is permanent.

The obvious lesson here is that the environmental forces that regulate HABs indeed are constantly changing.

FROM THE CONCEPTUAL TO THE MECHANISTIC

Moving from the conceptual to the mechanistic, one of the core needs for modeling HABs in eutrophic systems is an accurate estimate of nutrient loads entering receiving waters. There are a number of models that address various hydrological scales, for example, the Spatially Referenced Regressions on Watersheds (SPARROW; Robertson et al., 2009; Hoos and McMahon, 2009) and the Nutrient Export from Watersheds (NEWS; Seitzinger et al., 2005, 2010). Coupling nutrient discharge to the response of a single species or group of species requires models of receiving-water hydrologic properties for estimating retentiveness of the nutrient, as well as knowledge of the rates and pathways by which nutrients are consumed and recycled, and how such rates and pathways are affected by physicochemical factors. Ensembles of models and integrated ecosystem models that couple the atmosphere, land, and coastal ocean are required to quantitatively estimate nutrient transfer from air-shed to ocean, to investigate ecosystem response to climate changes, and

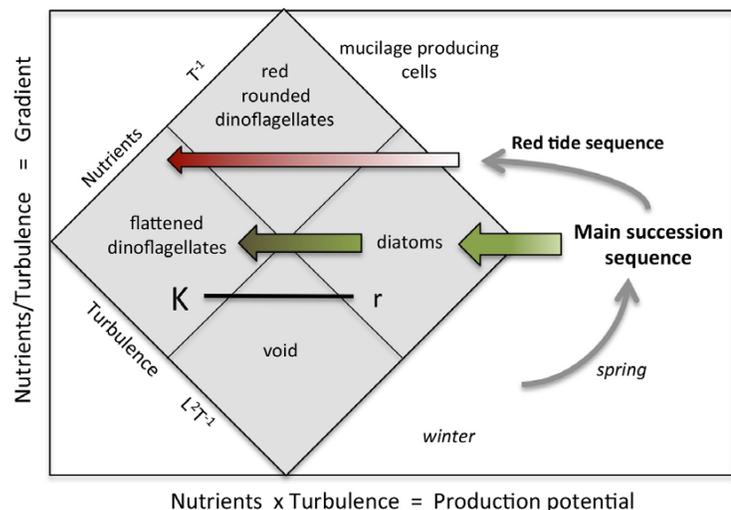


FIGURE 3. Margalef’s mandala. The mandala was developed from the original conceptual understanding of the trajectory of phytoplankton responses to nutrients and turbulence. The mandala illustrates both a generalized winter-spring bloom sequence and a “red tide” sequence. Figure redrawn from Margalef et al. (1979) and reproduced from Glibert (2016) with permission of Elsevier

to further explore the changes in HABs that are to be expected as eutrophication impacts increase.

Linking nutrient loads to HAB formation in models is especially difficult under conditions when mixotrophs dominate (which includes most conditions suitable for HABs). Such efforts are advancing (Flynn, 2010; Mitra et al., 2014), but ultimately forecast models must be at the same time robust and simple enough to be operational

and affordable to managers (Franks, in press). Because of the importance of varying nutrient stoichiometry, the minimum configuration of a model should consider multi-element descriptions as opposed to fixed Redfield constructs. Variable stoichiometric parameterizations in models must also begin to recognize that physiological processes and organismal stoichiometry can and do vary, even at growth-saturating substrate concentrations (Glibert et al., 2013).

SYNERGY WITH CLIMATE CHANGE

Human activities have substantially affected nutrient loads and composition, and the results of these inputs have also acted synergistically with other global changes. Climate change and nutrients interact in direct and indirect ways. Clearly, changes in temperature affect the habitat for HABs. Climate changes may further influence harmful algal species expansions due to altered precipitation patterns, including increases in droughts in some regions and/or increases in the frequency or intensity of storms in other regions. 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 (e.g., Heisler et al., 2008).

Climate change directly modifies temperature, which in turn affects HAB growth rates, motility, germination, pigment content, enzyme reactions, photosynthesis, and various other processes (e.g., Wells et al., 2015, and references therein). As a result, community composition is affected. Increasing temperatures positively affect those taxa with higher temperature optima for growth, while negatively influencing those taxa that have lower temperature optima. Increasing temperature disproportionately affects diatoms, as they generally thrive in colder seasons, and tend to have colder temperature optima than other microalgal groups. Moreover, the uptake of NO_3^- and its reduction to NH_3 generally decreases at higher temperatures, especially above 15°C – 18°C (e.g., Lomas and Glibert, 1999; Glibert et al., 2016), further suggesting that diatoms are negatively impacted as temperatures rise. In contrast, many cyanobacterial and dinoflagellate species, including HAB species, prefer warmer temperature conditions (e.g., Paerl and Huisman, 2008; Paerl and Scott, 2010). Temperatures also affect the community of organisms within which the harmful algal species may live, including

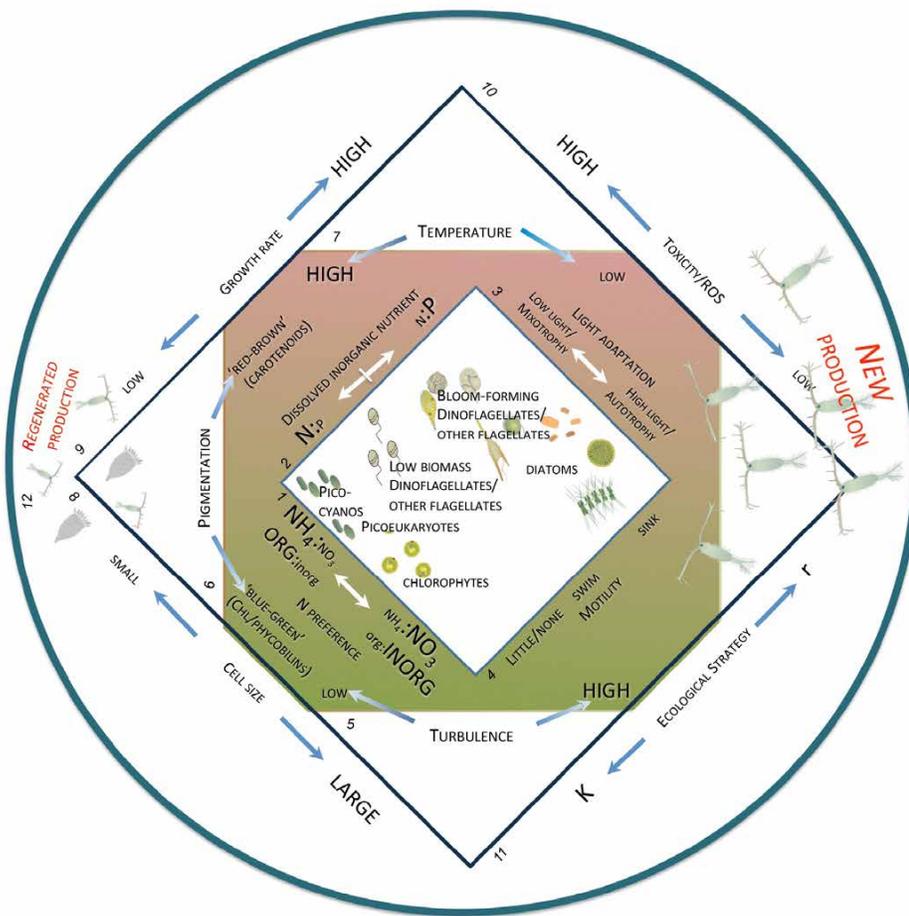


FIGURE 4. Revised phytoplankton mandala. Phytoplankton functional types are depicted along 12 axes (shown by the small numbers in the corners of the axes). The axes include: (1) the gradient of N forms preferentially used by the phytoplankton, from NH_4^+ to NO_3^- and/or from organic to inorganic forms; (2) the gradient of dissolved inorganic N:P available to the phytoplankton (the tic mark on the gradient arrow represents the Redfield proportion); (3) light availability and/or the propensity of the phytoplankton to be mixotrophic (herein generally meaning phagotrophic); (4) motility of the cells, ranging from no motility to swimming (flagellated) to cells with sink/float vertical migration strategies; (5) turbulence from low to high; (6) pigmentation of the cells, from higher relative proportion of carotenoids to higher relative proportion of phycobiliproteins and/or chlorophylls; (7) temperature, plotted on inverse scale from high to low; (8) cell size, from small to large; (9) growth rate from low to high; (10) propensity of the cells to be toxic or to produce other bioreactive compounds such as reactive oxygen, plotted on inverse scale from high to low; (11) ecological strategy along the K to r spectrum; and (12) propensity for the resulting production to cycle through either the microbial loop (regenerated production) or to constitute new production. Note that all scales are relative and no dimensions are implied. All responses within relative space are representative and are not meant to imply that all species or individuals within a given response surface will respond similarly. Reproduced from Glibert (2016) with permission of Elsevier

bacteria, viruses, competing phytoplankton taxa, and grazers (Wells et al., 2015, and references therein). The toxicity of many harmful algal species also increases with warming (Davis et al., 2010; 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 be associated with slower growth rates (e.g., Ogata et al., 1989; Lewis et al., 1993), but slower growth rates need not be detrimental to HAB formation if competitor species are also compromised.

EUTROPHICATION AND CLIMATE CHANGE: PAST AND PRESENT

The effect climate change has had on eutrophication is evident worldwide. One region where the expansion of HABs is unquestionable encompasses the Arabian Gulf and the Arabian Sea (Figure 5). As a result of the rise in piracy, which has affected scientists' ability to measure HABs from research vessels, ocean color satellite imagery has become invaluable in documenting these changes (e.g., Goes and Gomes, 2016). The scale of change

in eutrophication is massive. For example, the population of Mumbai, India, on the eastern coast of the Arabian Sea, has doubled in just the past decade with little advancement in sewage treatment. Swaney et al. (2014) also linked N inputs to Indian waters to excessive runoff of N fertilizer; fertilizer is consumed on adjacent lands at among the highest rates in the world, rates that increased 50% between 2000 and 2011.

Compounding the resulting major N pollution are large-scale changes in the regional oceanography. Summer monsoonal winds are now stronger than in past decades, bringing more nutrient-rich deep water to the surface. Receding snow cover from the Himalayas is resulting in stronger winds across the Indian subcontinent, intensifying the upwelling of nutrients off of Somalia, Yemen, and Oman (Goes et al., 2005). Consequently, beginning around 2000, the northern Arabian Sea has shifted from a winter phytoplankton assemblage that had previously consisted mostly of diatoms to a contemporary phytoplankton assemblage dominated by the large dinoflagellate *Noctiluca scintillans* (up to 2,000 μm in diameter; Gomes et al., 2014, and references therein; Goes and Gomes, 2016).

This HAB species is described as a colorless heterotroph, but it is actually a mixotroph; its blooms are green in color due to the presence of prasinophycean endosymbionts (*Pedinomonas noctilucae*). It relies upon the symbionts to fix carbon, and also ingests a variety of prey. These blooms were not observed during the Joint Global Ocean Flux Study (JGOFS) cruises of the early to mid-1990s (Gomes et al., 2008), but are now >300% more intense than in the late 1990s. As noted by Harrison et al. (2011) in a global review of *Noctiluca* blooms and their expansion, “*Noctiluca* may well be a coastal or offshore manifestation of eutrophication, a mixotroph responding to successional planktonic changes in nutrient availability.”

EUTROPHICATION AND CLIMATE CHANGE: THE FUTURE

The ability to predict how HABs may change with changes in nutrients or climate—at scales from local to regional to global—is critical to dealing with HABs in the future. There are numerous approaches for modeling the likelihood of HAB occurrence under future scenarios. One approach is highlighted here because it illustrates the potential benefits of applying the concept of nutrient ratios as important drivers in climate-forced projections. In this model, projections of the effects of climate and nutrient changes on the potential for expansion of specific harmful algal genera were made by applying a coupled oceanographic-biogeochemical model (Holt et al., 2009) combined with a suite of assumed physiological “rules” for genera-specific bloom development and habitat suitability (Glibert et al., 2014a). Habitat suitability was defined by a ratio of $\text{NH}_4^+:\text{NO}_3^-$ that exceeded 1, and an inorganic N:P ratio that was stoichiometrically imbalanced, together with genus-specific temperature and salinity criteria. Using the dinoflagellates *Prorocentrum* and *Karenia* spp. as examples, because they are globally common genera that are often associated with eutrophication, the

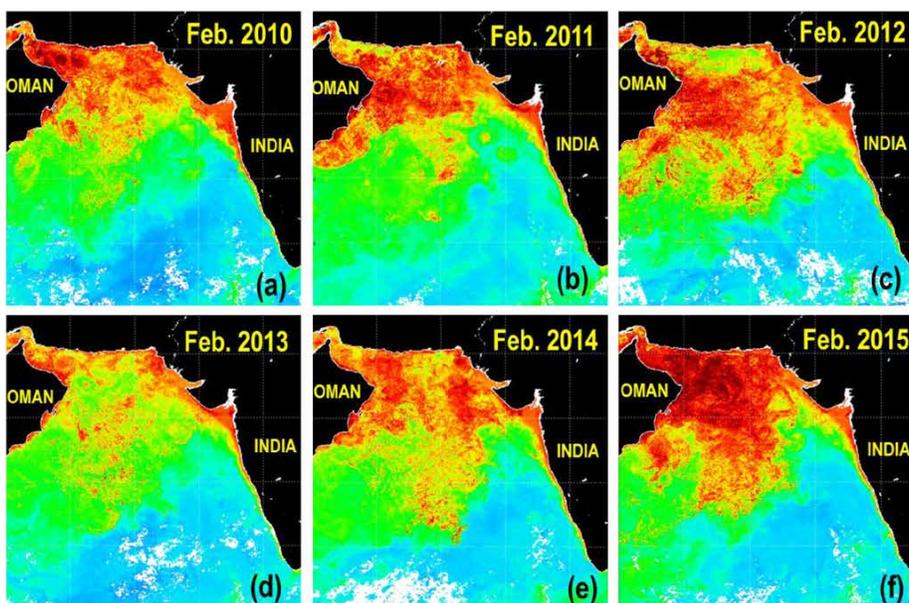


FIGURE 5. NASA MODIS-Aqua monthly composite images of chlorophyll *a* in the Arabian Sea showing the spatial expansion of *Noctiluca* blooms in February of 2010, 2011, 2012, 2013, 2014, and 2015. Reproduced and modified from Goes and Gomes (2016)

risk of future expansion was examined in several oceanographic regions, including the northwestern European Shelf-Baltic Sea system and northeastern Asia. Climate projections for “present-day” and “future” temperature scenarios were based on the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report (the “A1B” midline scenario; IPCC, 2007) during 1980–1990 versus 2090–2100, respectively.

The model output defined the fraction of time when all criteria were met, on a spatially explicit basis. In other words, for blooms to occur in the model scenarios, all criteria for growth (temperature, salinity, nutrient conditions) had to be met at the same time and location (Glibert et al., 2014a). Any scenario that altered one set of matching parameters in time or space without altering the other criteria led to a “mismatch” of conditions and a lesser likelihood for blooms to develop. This approach highlighted two important points. First, nutrient ratios (along with temperature and salinity) were used to define habitat criteria (rather than absolute concentrations of nutrients), and this approach was successful for *Karenia* and

Prorocentrum spp. in the studied regions. While absolute amounts set the total amount of biomass that could be supported, the proportions of nutrients were clearly important in defining “who” was there. Second, the model output indicated that bloom expansion (or contraction) depended not only on the change in abiotic conditions supportive of growth but also on the temporal or spatial match of expansion of those parameters.

Model projections indicated variable habitat expansion of *Karenia* spp. and planktonic *Prorocentrum* spp. HABs under the applied assumptions of climate change (Glibert et al., 2014a; Figure 6). Along the northern European coast, there was considerable expansion in the number of months each year that were conducive to both HAB genera, but this was most notable for planktonic *Prorocentrum*. The expansion of these HABs in future scenarios was less for the Asian coast, but there appears to be a northern geographic expansion. The projected increases in temperature and nutrient conditions suggest an even greater potential for expansion of these blooms, but the overlap of these conditions could

limit manifestation of these effects. A temporal mismatch in suitability of conditions for growth should not be viewed as evidence for limited potential for expansion. Rather, such a difference points to the possibility of expansion should there be a change in the timing of any one of the parameters. Climate forcing may alter the timing of nutrient loads relative to seasonal warming, which may in turn alter the alignment of suitable conditions. Overall, the model projections described here showed the future potential expansion for these two HAB genera in two large oceanic regions, and it is foreboding. Many factors are involved, and different species may show quite different projections. Nevertheless, collectively it is clear that the expansion of HABs, exemplified by *Karenia* spp. and planktonic *Prorocentrum* spp. in some regions, is likely to continue in the coming years.

LESSONS EMERGING AND CONTINUING CHALLENGES

Several simple lessons emerge from the work of the past decade with regard to HABs and nutrients. The global expansion of HABs is real and is a consequence

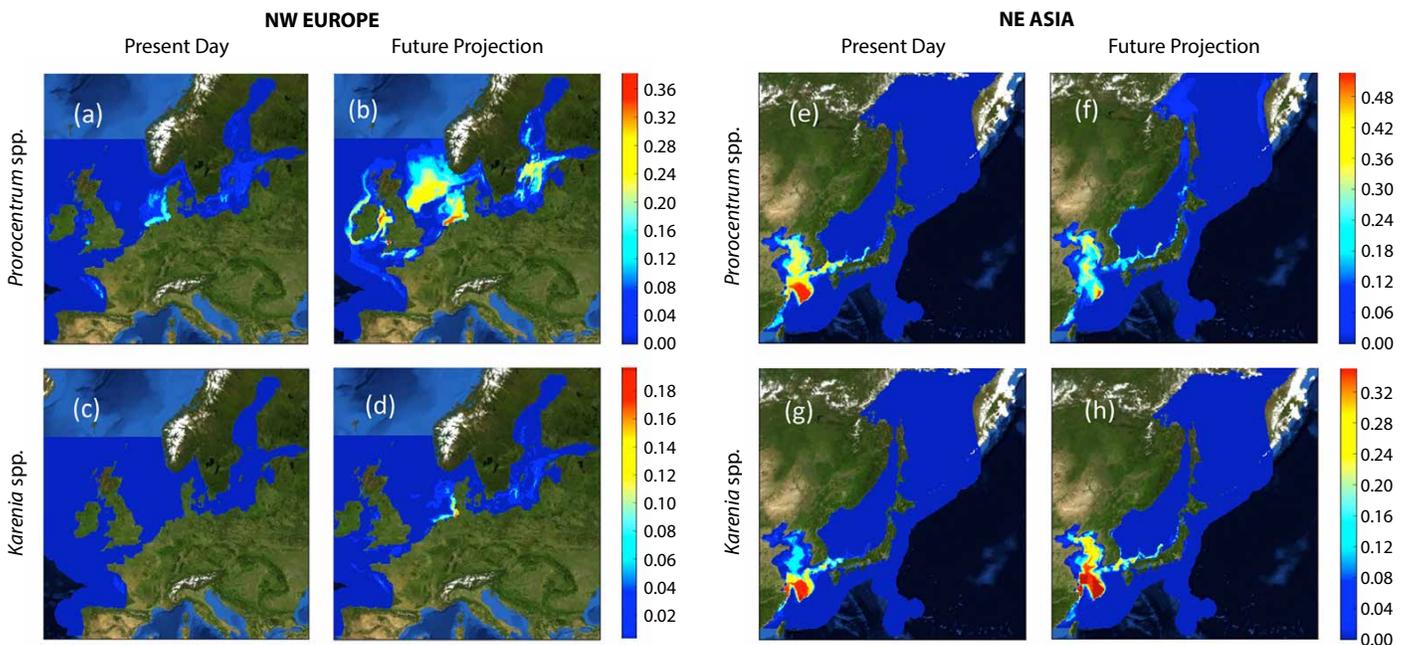


FIGURE 6. Output of the coupled oceanographic-biogeochemical model described for the northeast European/Baltic Sea region. Panels (a) and (b) depict the spatial distribution of habitat suitability (spatially explicit fraction of time of year for which all suitable conditions were met) for *Prorocentrum* spp. for present (encompasses period from 1980 to 1990) and future conditions projected using A1B IPCC (2007) scenarios for climate change (encompasses period from 2090 to 2100). Panels (c) and (d) are the same except for conditions suitable for *Karenia* spp. Panels (e)–(h) are the same, except for northeast Asia. Reproduced and modified from Glibert et al. (2014a) with permission of Wiley & Sons Inc.

of increasing nutrient loads to land, sea, and air and the many pathways by which these nutrients leach to fresh and marine waters. Anthropogenic activities that directly or indirectly affect nutrient availability for HABs include not only our insatiable demand for nutrients but also other anthropogenic factors that affect nutrient availability, forms, and proportions. Overfishing and intensive aquaculture, changes to the hydrodynamics of major river systems and flow due to dam construction, and increasing consumptive water demands also alter nutrient availability, as do activities that affect climate.

There is much work to be done to understand physiological ecology across function groups, including parameterizing rates and characterizing traits and determining how they are externally driven and internally dynamically regulated. That nutrition plays an important role in the expansion of HABs should be obvious with our contemporary understanding of phytoplankton physiology and ecological stoichiometry. Nutrient changes do not need to be full-throttle eutrophication impacts (hypoxia) for habitats to promote HABs. Even relatively small changes in nutrient supply can substantially affect many important properties of the ecosystems. Simplistic approaches to curb HAB growth by continuing to reduce the “limiting” nutrient fail to advance us from a dose-response mindset; as emphasized here, stoichiometry changes do matter for biodiversity. It is time to put to rest the argument that single nutrient controls will be effective in curbing HABs. HABs may thrive at either end of the continuum of N to P limitation, and they can become more toxic at either end of the N:P continuum. Curbing one nutrient may help to reduce biomass but may not change or may even accelerate a trajectory of change in biodiversity. Dual nutrient reduction strategies are advocated here as well as elsewhere in the literature (Conley et al., 2009; Glibert et al., 2014b; Paerl et al., 2016).

While the challenges of controlling

nutrients and managing HABs will continue to be great, there are also many opportunities to advance understanding of HABs and environmental changes. This brief overview cannot capture all the many advances that have been made in our understanding of HABs and their relationships with nutrients. What has been highlighted here are advances in understanding the physiology and the nutrition of these fascinating organisms. They interact in communities on many levels. Grazing effects, allelopathy, and biogeochemical fluxes are part of the suite of environmental factors regulating their growth. The plasticity of nutritional pathways, as well as the plasticity of food web interactions, including mixotrophy, creates immense challenges for model constructs. Capturing dynamic behavior will continue to be a challenge (Kana and Glibert, 2016), as many traditional biomass-based models are incapable of describing trophic interactions correctly because of the implications of variable stoichiometry and, for HAB species, the implications of the accumulation of noxious chemicals during nutrient stress (Mitra and Flynn, 2005, 2006).

Understanding the full suite of processes and factors that underlie variable stoichiometry at all scales—and for elements beyond N and P emphasized here—and the feedbacks between them is a grand challenge (Frigstad et al., 2011). Climate change, altered CO₂ levels, and their implications for altered productivity of the global ocean should motivate both new dynamic balance model architectures and new experimental investigations that support them. Based on the knowledge we have in hand, the management implications are clear: the most effective actions to reduce HABs and their impacts will be continued efforts to reduce nutrients. New management approaches that focus on dual nutrient (N,P) control and regulation of nutrient forms will be required for effective management of HABs. 

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ACKNOWLEDGMENTS

We dedicate this paper to the memories of Yves Collos and Paul J. Harrison, who contributed substantially to efforts to understand the physiological ecology of HABs and their nutrient requirements. This paper benefited from the many contributions to the GEOHAB Open Science Meetings on HABs and Eutrophication, work conducted by SCOR working group #132 on Land Based Nutrient Pollution and Harmful Algal Blooms, and by a Leverhulme Trust International Network Working group on Mixotrophy. We wish to especially thank Mingjiang Zhou, Lex Bouwman, Arthur Beusen, J. Icarus Allen, Kevin Flynn, Aditee Mitra, and Joaquim Goes for their contributions to GEOHAB and related programs on nutrients and HABs that have been highlighted here. This is a contribution of the GEOHAB Core Research Project on “HABs and Eutrophication” and contribution number 5317 from the University of Maryland Center for Environmental Science.

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ARTICLE CITATION

Glibert, P.M., and M.A. Burford. 2017. Globally changing nutrient loads and harmful algal blooms: Recent advances, new paradigms, and continuing challenges. *Oceanography* 30(1):58–69, <https://doi.org/10.5670/oceanog.2017.110>.