

Chapter 12

Key Questions and Recent Research Advances on Harmful Algal Blooms in Relation to Nutrients and Eutrophication



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12.1 Introduction

Changing nutrient loads and increasing levels of atmospheric CO₂ are significant drivers of our “ever-changing world,” and their adverse effects on aquatic biodiversity and ecosystem health are well documented (e.g., Cloern 2001; Howarth et al. 2002; Heisler et al. 2008; Doney 2010; Glibert et al. 2014a; Glibert and

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Burford 2017). Human activities, such as the use of synthetic fertilizers, energy production, and expansion of industrialized agriculture, aquaculture, and concentrated animal operations, have had tremendous impacts on the global cycling of nutrients and carbon (C) on land, in freshwaters, and in coastal waters (e.g., Smil 2001; Galloway et al. 2002; Doney 2010; Bouwman et al. 2011, 2013b). Coasts are “peopled seascapes,” and, through their complex relationships with the oceans, people “pollute and build in the coastal zone, consume seafood and thereby support excessive fisheries, extract and burn fossil fuels and contribute to global change” (Shackeroff et al. 2009). An important consequence of such activities in aquatic systems is eutrophication. This results in harmful algal blooms (HABs) that can produce toxins, cause fish kills directly or through the formation of hypoxia/anoxia, alter trophic interactions and broadly affect food webs and biodiversity, and potentially impact human health through various routes of exposure (GEOHAB 2001). As recognized in the special issue of *Harmful Algae* on Eutrophication and HABs that was published in 2008, the complexity of the relationships between HABs and nutrients has been well recognized (Glibert et al. 2008a):

Historically, our conceptual understanding of the relationship between nutrients and HABs was based upon the simplistic notion that more nutrients should yield higher algal biomass in a direct relationship. The frame of reference was restricted to noticeable blooms whose biomass was linearly related: if such high –biomass blooms did not occur, the HAB species was deemed unrelated to nutrient enrichment. Within the past decades, insights have advanced considerably. There is greater appreciation for interactive influences of the composition and relative proportion of availability of nutrient pools, the range of physiological responses by different phytoplankton species and functional groups, and the interactions of other dynamic factors such as physics and grazing in controlling responses to cultural eutrophication by HAB and other algal populations. It is now recognized that HAB species can be directly and/or indirectly stimulated by nutrient over enrichment, and that chronic, subtle effects can be equally important or even more important than the obvious, acute effects. And, it is recognized that nutrient enrichment interacts with other major drivers, such as climate change, in both direct and indirect ways.

These statements ring equally true today, and these complexities have been extensively described, and much more is now understood regarding the many interactions and factors related to nutrients and HABs (e.g., Glibert and Burford 2017).

The GEOHAB Core Research Project (CRP) on HABs and Eutrophication, launched in 2005, fostered two international Open Science Meetings (Baltimore, Maryland, USA, 2005, and Beijing, China, 2009), bringing researchers together with expertise ranging from algal physiology to global modelling of nutrient exports. The GEOHAB Report on HABs in Eutrophic Systems (GEOHAB 2005) laid out a number of key questions that required international, collaborative efforts. These key questions and their progress are summarized in this chapter, along with a summary of areas that need further attention, recognizing that progress has been enormous and only a few highlights can be given in this short chapter. The work of the CRP on HABs and Eutrophication was further augmented by the formation of a Scientific Committee on Oceanic Research (SCOR) Working Group on Land-Based Nutrients and HABs. Given the pace at which nutrient loads continue to

pollute the global landscape and the global expansion of HABs, continued international collaborative efforts in understanding changing nutrients and their relationships with HABs are not only necessary, but urgent.

12.2 Key Question 1: Are There Clusters or Specific Types of HAB Species that Are Indicative of Global HAB Increases?

There are clear examples of HAB genera that have increased in concert with eutrophication, and several are highlighted here. Among the species for which there is considerable evidence of a direct eutrophication relationship is *Prorocentrum minimum* (Heil et al. 2005; Glibert et al. 2008b, 2012). These global relationships underscore what has been well recognized at the regional scale: nutrients and organic loads from land-based sources promote the growth of *P. minimum*. In the Baltic Sea, the Black Sea, the Chesapeake Bay, and the Neuse River Estuary of the Albemarle-Pamlico estuarine system in the southeastern USA, long-term records of phytoplankton assemblage composition provide strong support that this species has flourished as these systems became increasingly eutrophic (Marasović et al. 1990; Moncheva et al. 1995; Heil et al. 2005; Hajdu et al. 2005; Pertola et al. 2005; Tango et al. 2005). A recent assessment of *P. minimum* in the Baltic Sea has linked its expansion in time and space, and its ecosystem impacts with human activities and associated nutrient pollution (Olenina et al. 2010). There are numerous descriptions of this species proliferating in waters influenced by freshwater inputs, especially freshwaters laden with organic forms of nutrients (e.g., Silva 1985; Granéli et al. 1985, 1989; Stonik 1995). In South Australia, *P. minimum* blooms have been documented near sewage outfalls (Cannon 1990). Blooms in the Navichiste Lagoon Complex on the east side of the Gulf of California have been linked to high NO_3^- and NH_4^+ in offshore waters (Martinez-Lopez et al. 2008). Along the coast of Mexico, where *P. minimum* only became established about 30 years ago, most blooms are associated with nutrient-rich shrimp ponds or other aquaculture (Sierra-Beltran et al. 2005), and similarly in Queensland, Australia, such blooms have also been reported in intensive, eutrophic shrimp ponds (Burford and Pearson 1998).

The global expansion of *P. minimum* and its relationship to nutrients has been documented using spatially explicit global maps of nutrient pollution (see also Sect. 12.6). Global nutrient data, derived from the Global Nutrient Export from Watersheds (Global NEWS) effort (Seitzinger et al. 2005; Dumont et al. 2005; Harrison et al. 2005a, b), allowed identification of relationships between documented occurrences of *P. minimum* and nutrients as total nitrogen (TN) and phosphorus (TP) export (Fig. 12.1a, here, illustrating trends for N only), and by dominant form of N, as sewage, fertilizer, manure, or fixation of atmospheric sources (Fig. 12.1b), and the extent to which the export of dissolved organic N (DON)

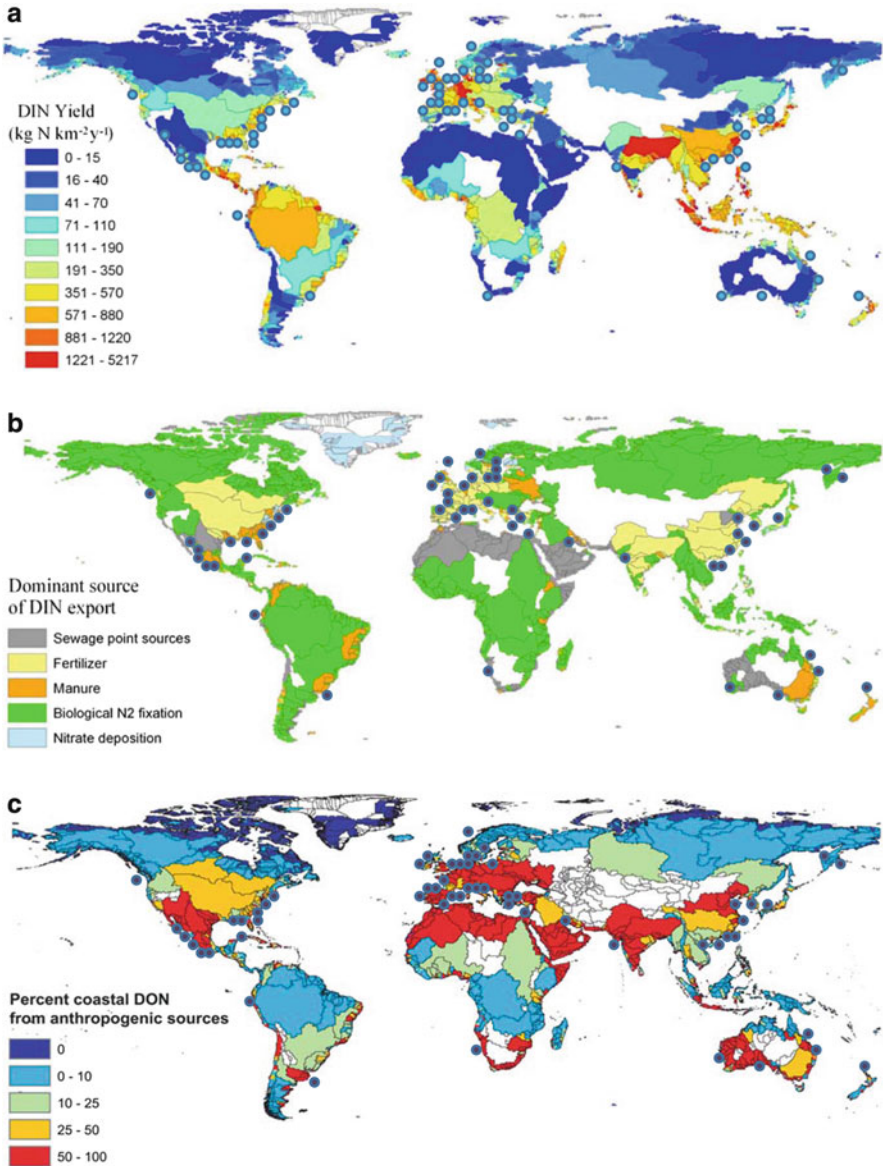


Fig. 12.1 (a) Global NEWS model of DIN yield by watershed (kg N km⁻² year⁻¹) by exoreic basins (from Dumont et al. 2005); (b) dominant source of DIN export in exoreic basins as predicted by the Global NEWS models (from Dumont et al. 2005); and (c) percent anthropogenic contribution to DON export from exoreic basins as estimated from Global NEWS models (from Harrison et al. 2005a) and the global distribution of *P. minimum* indicated by circles (from Heil et al. 2005). Figures reproduced from Glibert et al. (2008b) with permission from the publisher

was attributable to anthropogenic sources [Fig. 12.1c; Glibert et al. 2008b; see also Chap. 4, Glibert et al. (2018)].

Among the most spectacular examples of the association between harmful planktonic *Prorocentrum* species and eutrophication is the recent development of massive blooms of the related species, *P. donghaiense*, along the coast of China, especially the East China Sea, in the region formed by the convergence of the Yangtze (Changjiang) River plume and the Taiwan Warm Current [Lu and Goebel 2001; Zhou et al. 2003, 2008; Lu et al. 2005; see also Chap. 15, Yu et al. (2018)]. Such blooms were not reported until 1995 (Lu et al. 2005), but massive blooms, up to 10,000 km² in areal extent, have occurred in late spring virtually every year since, and the bloom of 2005 was particularly well studied (Zhou et al. 2008; Li et al. 2009, 2010; Lu et al. 2011). The rapid rise in the export of N from the expansion of fertilizer use in the Changjiang River watershed has been strongly associated with the expansion of these blooms (Zhou et al. 2008; Li et al. 2009). This area is the most developed in China, with over 440 million people living in the watershed (Li et al. 2009). The annual dissolved inorganic N (DIN) load from coastal waters influenced by the Changjiang River has reached 1.4×10^6 t, which is higher than DIN loads from the Mississippi or Amazon rivers (Goolsby and Battaglin 2001; Duan et al. 2008; Li et al. 2009). Blooms form when the N-rich, but comparatively P-poor, Changjiang River plume mixes with upwelled water from the Taiwan Warm Current, which is comparatively P-replete (Tang et al. 2000; Fang 2004), forming a front where the N:P ratio is suitable for growth (Li et al. 2009). Blooms of *P. minimum* and *P. donghaiense* are also now a regular feature in the southern waters of Korea (Lee and Kim 2008; Lu et al. 2011). These blooms have been linked to fish and shrimp kills with considerable economic consequences (Lee and Kim 2008).

The dinoflagellate *Cochlodinium (Margalefidinium) polykrikoides* represents another clear example where there has been global expansion, and blooms appear to be related to nutrient pollution. This species is now widespread, from the western Pacific to the eastern Atlantic, the Indian Ocean, the Arabian Gulf, and the Mediterranean (Kudela et al. 2008b; Matsuoka et al. 2010; Kudela and Gobler 2012). As a fish killer, it has become particularly problematic in regions where aquaculture has expanded, such as Korea and Japan where it has caused considerable economic damage (GEOHAB 2010). In the USA, it has become a recurrent late-summer bloom former in Chesapeake Bay (e.g., Mulholland et al. 2009) and in other east coast lagoons when seasonal storms deliver a pulse of nutrients to the estuary. In the Arabian Gulf, a massive nearly 9-month-long *C. polykrikoides* bloom occurred in 2008–2009 and ultimately stretched from Oman to coastal Iran and caused fish kills as well as impacts to desalination plants throughout the region (Richlen et al. 2010; Al-Azri et al. 2014; Fig. 12.2). It is not clear what triggered this bloom in this particular year, nor why *Noctiluca scintillans*, the more frequent bloom former in the region over the past decade, was supplanted. A common feature of the antecedent nutrient conditions of this and other *C. polykrikoides* blooms is that phosphate (PO_4^{3-}) concentrations were on average 50–100% higher than in non-bloom sites, and waters were comparatively enriched in ammonium (NH_4^+) rather than nitrate (NO_3^- ; Al-Azri et al. 2014).

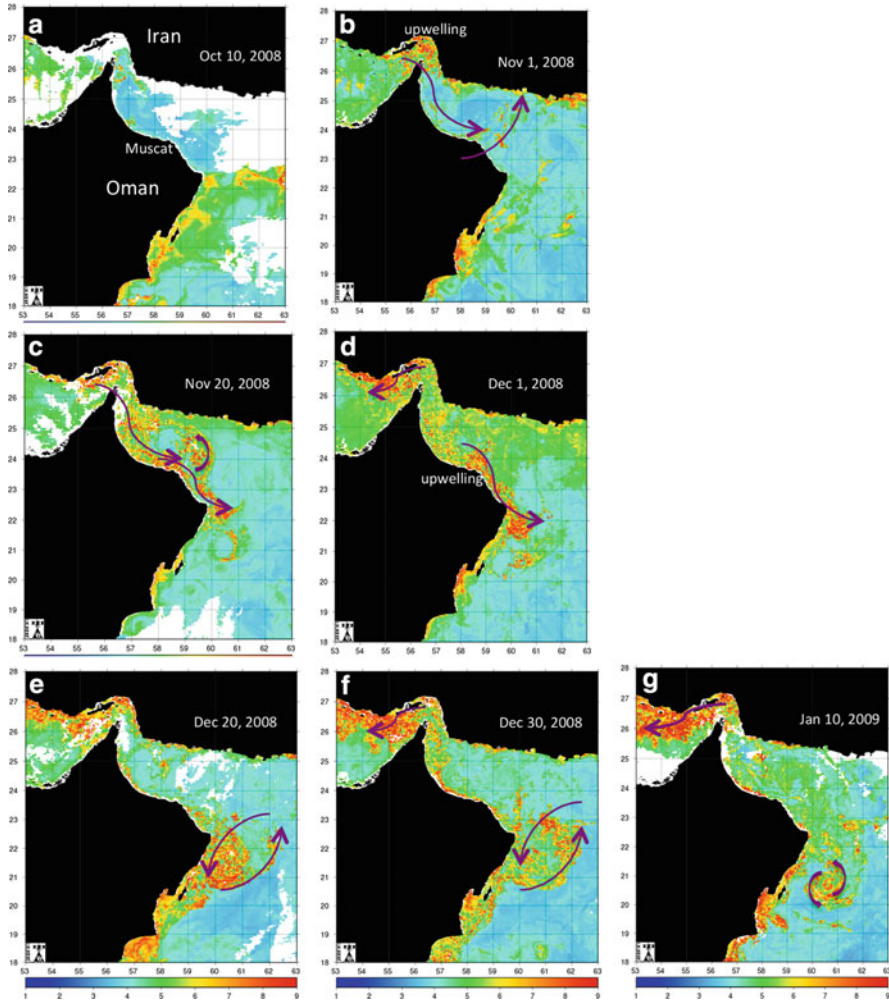


Fig. 12.2 (a–g) Satellite images showing the development of blooms in the Sea of Oman and Arabian Sea in 2008 and their dissipation in January 2009. The *arrows* superimposed on the images are intended to draw attention to the major mesoscale features and are not meant to imply measured flow. The chlorophyll scale on the images is intentionally reported dimensionless to underscore the relative patterns, not absolute biomass accumulations. Figure reproduced from Al-Azri et al. (2014) with permission from the publisher

Moreover, the mixotrophic properties of this species have long been known (Larsen and Sourmia 1991; Jeong et al. 2004). Its growth rate has been shown to increase by almost a factor of two when growing mixotrophically, compared to phototrophically (Jeong et al. 2004). It is thus likely that *C. polykrikoides* derives a substantial fraction of its nutrition via mixotrophy during its blooms.

Clearly the evidence is broad and deep that HABs are expanding globally in concert with increasing nutrient loads. That certain taxa should be favoured under some nutrient enrichment conditions should be of no surprise, given the suite of adaptive strategies of many HABs related to nutrient availability, proportion, and form (e.g., Heisler et al. 2008; Glibert and Burkholder 2011; Glibert and Burford 2017, and references therein). The question of whether there are HAB species that track anthropogenic nutrient changes is clearly answered; what needs more thorough elucidation is the specific adaptations of these species that allow them to thrive under such conditions (e.g., Glibert and Burkholder 2006; Glibert and Burford 2017).

12.3 Key Question 2: To What Extent Do Residence Time and Other Physical Processes Impact the Relationship Between Nutrient Loading and HAB Proliferation?

There is considerable evidence that residence time and hydrodynamics affect the relationships between nutrients and HAB proliferation. These relationships are mainly mediated through the forms of nutrient that are either delivered primarily with freshwater flow or are promoted through water-column retention. A global review of estuarine coastal typology has highlighted the differences in nutrient retention between different types of coastal features and between different nutrients [N and P; Dürr et al. 2011; see also Chap. 4, Glibert et al. (2018)]. Not only are the differences in nutrient retention between different estuarine types substantial, but there is a general trend towards increased retention at higher latitudes (Laruelle 2009). Water-column retention is also being altered globally through the construction of dams and reservoirs as well as coastal alteration through construction of harbours and artificial canals for residential development.

One of the clearest examples of flow relationships with the propensity for HABs comes from the comparison of river-dominated estuaries versus coastal lagoons (Glibert et al. 2010). Coastal lagoons represent a class of estuary characterized as shallow, highly enclosed, and typically quiescent in terms of wind, current, and wave energy relative to their deeper, more dynamic counterparts, river-dominated estuaries (Madden et al. 2010). Coastal lagoons also tend to have high surface to volume ratios and can have high wetland area to water volume ratios as well (Bricker et al. 2007; Madden et al. 2010). Differences in the quality of the nutrient pool, the seasonal timing of the delivery and source of nutrients, as well as in the resident phytoplankton community can lead to fundamentally different types of algal blooms in coastal lagoons than in river-dominated estuaries. Lagoonal blooms are often dominated by picoplankton, such as *Aureococcus anophagefferens*, which has bloomed in the lagoons of Long Island, NY, and Maryland Coastal Bays, USA, and more recently the Bohai Sea [see Chap. 15, Yu et al. (2018)]. In fact, blooms of a related species, *Aureoumbra lagunensis*, which occurred in Laguna Madre, Texas,

USA, in the 1990s, lasted nearly 9 years (Buskey et al. 2001). Another example is *Synechococcus elongatus*, which has formed massive blooms in Florida Bay, USA, and these blooms may be also sustained for long periods of time. High-biomass picoplankton blooms in lagoons may reach near monospecific proportions. During blooms in Florida Bay in 2002 and 2005, for example, *Synechococcus* spp. comprised >99% of the phytoplankton assemblage and reached 10^8 cells L^{-1} (Glibert et al. 2004; Hitchcock et al. 2007). Similarly, in the Chincoteague Bay, USA, *A. anophagefferens* has been found to comprise 85–95% of the phytoplankton community during bloom periods (e.g., Wazniak and Glibert 2004). Sustained blooms of picoplankton such as these have been termed ecosystem disruptive algal blooms (EDABs; Sunda et al. 2006). Blooms in river-dominated estuaries, by contrast, tend to be highly seasonal and dominated by larger-sized phytoplankton (i.e., >10 μm), typically diatoms. Furthermore, blooms in lagoons tend to be supported by regenerated nutrients that may be lower in concentration but which are made available through higher regeneration rates from both water-column and benthic processes. Highest phytoplankton biomass in riverine systems generally occurs in the spring, following maximum runoff, mainly of NO_3^- (e.g., Pennock 1985; Malone et al. 1996). Only in summer do temperate river-dominated systems resemble those of coastal lagoons when temperature is warm, flow is reduced, and the spring diatom bloom begins to be succeeded by flagellates, cyanobacteria, and other picoplankton that thrive on the nutrients regenerated from the spring bloom (Malone et al. 1996). Episodic blooms of large dinoflagellates occur in both types of systems but are generally not long-lived.

Anthropogenic activities are also altering hydrology in many regions, which in turn leads to changes in nutrient export to aquatic systems. River discharge is being altered throughout the world due to dam construction and water abstraction. Dams of a capacity of more than 1 MW that have been constructed, or are under construction, number in the thousands (Zarfl et al. 2015), and extremely large dams (with capacity of >1 GW) 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 HABs [see also Chap. 4, Glibert et al. (2018)]. In addition to the reductions in overall river flow that occurs from dam construction, large river systems 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 also alters nutrient loads and proportions in downstream waters (Beusen et al. 2016). For example, retention of Si upstream, following construction of the Three Gorges Dam in China, has been considered to be an important factor leading to altered nutrient proportions favouring HABs in East China Sea (e.g., Zhang et al. 2015).

Many estuaries have controlled flow to meet management goals, but these controls have flow on effects on nutrients. Estuarine flow is also highly regulated in the San Francisco Bay Delta (Kimmerer 2002; 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 community 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; Glibert et al. 2011), a consequence of managed flow, increased pollution by N, and altered grazing communities. Another example from the USA where flow has been substantially altered by human activities is that of the Everglades, Florida. In the 1940s, much of the natural flow was channelized and redirected. New efforts to restore the Everglades is resulting in higher flows of freshwater to the northern regions of Florida Bay, and this is having some effects on the phytoplankton assemblages there as well (e.g., Shangguan et al. 2017).

Important lessons emerge from these examples. Systems that naturally differ in their typology, and therefore in their nutrient retention, can create differing conditions for HABs, based on both total nutrient loads and the forms of nutrients that result. Altered flow, including the many mechanisms by which flow is being anthropogenically changed, also alters nutrients, in terms of total loads and proportions, and these changes can create “windows of opportunity” for HABs to develop or at least create conditions where phytoplankton assemblages change in composition.

12.4 Key Question 3: How Do Feedbacks and Interactions Between Nutrients and the Planktonic, Microbial Food Web Impact HABs and Their Detrimental Effects?

Grazer interactions and other feedbacks within the microbial food web are complex and clearly contribute to HABs. The clearest effect is when there are reductions in grazer abundance that might result from direct or indirect interactions with HABs. Local reductions in grazer abundances may also be in direct response to HABs (e.g., avoidance or mortality induced by the HABs, Granéli and Johansson 2003) or in response to the effects of past HAB events. The responses of zooplankton and other grazers of toxic algae are often species-specific in terms of behavioural responses and toxin susceptibility. Zooplankton impaired by ingesting harmful algae may also be more susceptible to predation and thus may become important vectors for transferring toxins in the pelagic food web. Alternatively, zooplankton faecal pellets may be important sources of toxin to benthic communities. Herbivorous fish can accumulate and transfer toxins and even cause mass mortalities of the marine birds that consume them. During food web transfers, toxins may be bioaccumulated, excreted, degraded, or structurally modified. In order to understand the effects of HAB species on the marine food web, both the direct as well as

the indirect, more subtle pathways by which toxins are transferred and transformed, and the differential susceptibility of marine organisms to these toxins must be characterized. In some cases, HABs may insult, but not kill, other members of the food web, leaving them stressed and therefore more susceptible to other sources of mortality, such as infection by pathogens. Burkholder et al. (2018) have published a comprehensive analysis of food web effects of HABs.

Nutrients have important cascading effects through the food web. Phytoplankton vary in terms of lipid and protein content and also in terms of elemental stoichiometry. The net effect of the stoichiometric regulation of consumers, together with different nutrient requirements of phytoplankton, is that not only are grazers affected by food quality, they, in turn, affect food quality by altering the composition of nutrients available to them through nutrient recycling (Sterner and Elser 2002). Grazers release nutrients directly, but they also consume the primary consumers of nutrients, and other grazers, which are also nutrient regenerators (Glibert 1998). Whether grazers are highly constrained or more flexible in their stoichiometry has large consequences for nutrient regeneration, as those grazers that are highly constrained will, by necessity, regenerate the nutrients that are consumed but not needed to maintain their biomass. By regenerating the nutrients not needed, but retaining the nutrients that are needed, positive feedbacks are developed (Elser et al. 2000; Sterner and Elser 2002). For example, in principle, grazers with strict stoichiometry feeding on phytoplankton that are N-rich will excrete proportionately more N than those grazing on phytoplankton that are more balanced in their N:P or N:C ratio. By excreting more N, the condition of excess N is maintained for the phytoplankton (Sterner and Elser 2002). Such a condition creates wide variations in the stoichiometry of producers and consumers and presents further cellular challenges for producers to regulate both the limiting and saturating nutrient cellular levels. Preferential grazing will also affect the flow of regenerated nutrients. This can create the potential for shifts in dominant bloom species. This process of stoichiometric interaction is seen at all levels of the food web, leading to a complex interaction of stoichiometry and trophic cascades.

An important food web interaction at the microbial level, often involving HABs, is mixotrophy [see also Chap. 7, Flynn et al. (2018)]. Many different types of HAB species that thrive in eutrophying or eutrophic estuarine and coastal marine habitats, including cyanobacteria, dinoflagellates, and ochrophytes (diatoms, golden flagellates, brown tide algae, and raphidophycean flagellates), are mixotrophs (Burkholder et al. 2008). Most phytoflagellates (heterokontophytes, haptophytes, and cryptophytes) are capable of consuming bacteria and small eukaryotic cells (Unrein et al. 2007; Zubkov and Tarran 2008; Stukel et al. 2011). Dinoflagellates exhibit a wide range of capabilities, from those that express phagotrophy only upon extreme nutrient starvation to exclusive phagotrophic forms. Even the latter organisms may gain at least a transitory advantage from ingestion (Raven et al. 2009; Jeong et al. 2010; Hansen 2011) or other mixotrophs (Minnhagen et al. 2011). It is also apparent that the stoichiometry of predator and prey quality also has strong effects on the success of mixotrophs (Lundgren et al. 2016; Lin et al. 2017). The mixotrophs, *Prymnesium parvum* and *Karlodinium veneficum*, have both been

shown to graze differentially on prey depending not only on their nutritional condition but also that of the prey, preferring prey that may help them to balance their nutritional requirements (i.e., the mixotroph in a high N condition will preferentially graze on prey in a comparatively high P condition and vice versa; Lundgren et al. 2016; Lin et al. 2017).

Importantly, it appears from several studies that mixotrophy also may permit growth to be sustained or even accelerated during periods of apparent water-column nutrient deficiency or imbalance. The benefits of mixotrophy for the dinoflagellates *C. polykrikoides* were noted above. The same growth advantage has been observed for *Karenia brevis*. Toxic *K. brevis* has been found to graze on the cyanobacterium *Synechococcus* sp., as well as on cryptophytes (Jeong et al. 2005; Adolf et al. 2008a; Glibert et al. 2009a). In laboratory experiments, it has been shown that *K. brevis* can graze from ~1 to 80 *Synechococcus* cells h⁻¹ (Jeong et al. 2005; Glibert et al. 2009a), depending on the predator/prey ratio, with the growth rate of *K. brevis* increasing as the supply of *Synechococcus* increased. In contrast, *P. parvum* (as *Prymnesium patelliferum*) and *Chrysochromulina* spp. that ingested prey under light- and nutrient-sufficient conditions maintained similar growth rates with versus without phagotrophy (Larsen et al. 1993). It is clear that many mixotrophs increase their feeding when in a condition of nutrient imbalance, but strict nutrient limitation is not necessary. Moreover, there is much to be done to fully understand the relationships between mixotrophy and toxin production, which may be synergistic.

In all, factors such as the relative availability of the N (P and C) substrates, the nutritional status of the component organisms, and the number of trophic interactions, along with environmental parameters such as ambient light and temperature, all determine the extent of the dynamic metabolic balance in the use of one substrate vs another and, in turn, the relative success of (or not) of primary producers—including HABs—and their consumers. Once the balance is tipped, a new dynamic emerges. That nutrition plays a key role in this process should be obvious with our contemporary understanding of phytoplankton physiology and ecological stoichiometry; unravelling the multifaceted effects of nutrients, trophodynamics and HABs in an imbalanced and otherwise dynamic system will continue to present many challenges to be addressed in the future (Glibert 2017).

12.5 Key Question 4.0: Do Anthropogenic Alterations of the Food Web, Including Overfishing and Aquaculture Activities, Synergistically Interact with Nutrients to Favour HABs?

The interactions of trophodynamics and HABs at the lower end of the food web are also altered in complex ways when the upper levels of food webs are changed due to reductions in fish pressure, on the one hand, through overfishing or, on the other

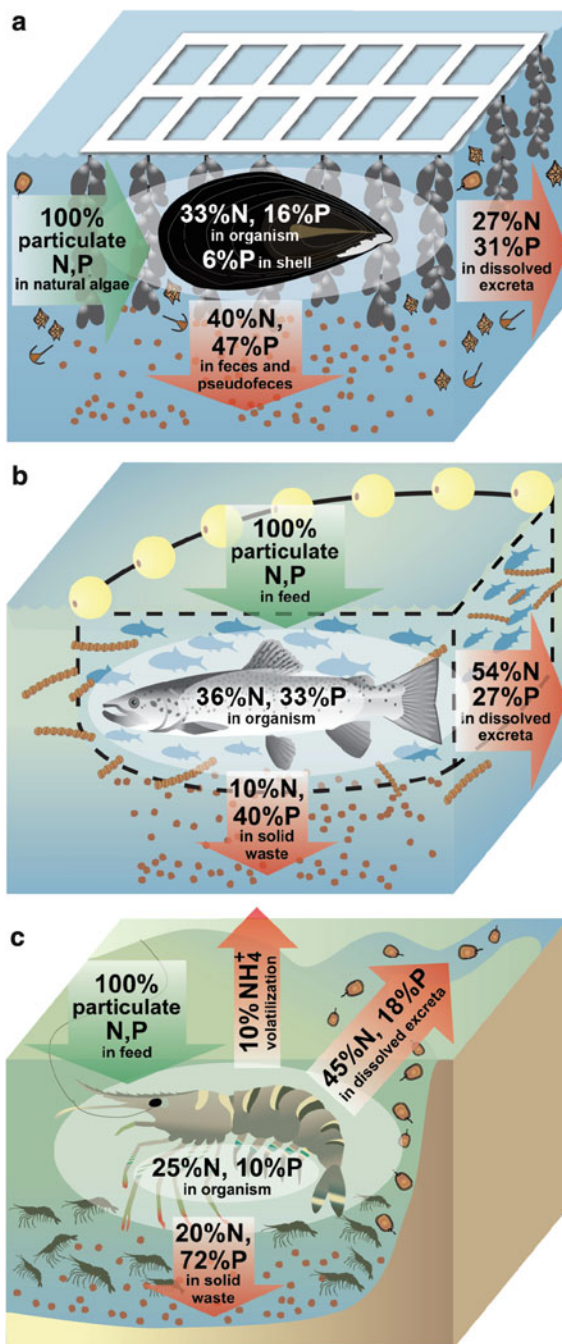
hand, through enhancement of fish (or shellfish) abundance through aquaculture. While these effects are many, the key aspect summarized here is how fish (or shellfish) abundance alters the availability and composition of nutrients that may, in turn, support HABs.

As outlined above, grazers alter the rate of nutrient regeneration and can alter the composition of that nutrient. The regeneration of nutrients from higher trophic levels becomes an increasingly important pathway when animals are at densities above that found in their natural habitat, as is the case with aquaculture. With regard to aquaculture impacts, all intensive culture systems alter the natural cycling of nutrients, with increased release of dissolved nutrients and solid excreta compared to natural environments, as well as the potential alterations of sediment biogeochemistry (Honkanen and Helminen 2000; Wu et al. 1994). Efficiency of nutrient retention by the reared organisms is on average 35% (Bouwman et al. 2013a; Fig. 12.3). In systems with exogenous feed addition, there is also breakdown of undigested feed. Estimates of dissolved and particulate N and P release, based on modelling that accounts for feed practices and conversion ratios by species (Bouwman et al. 2011, 2013b), show that dissolved nutrients are more N-rich, but particulate nutrients tend to be more P-rich in finfish systems and crustacean ponds than molluscan culture. Nutrient release products also vary considerably from the Redfield ratio (Redfield 1934). Further alteration of nutrient concentrations and stoichiometry results due to fluxes of N and P from sediments to water via remineralization of nutrients in excess feed, faeces or pseudofaeces (Burford and Longmore 2001).

The different release products, their forms, and proportions, in different aquaculture conditions, may contribute to which algal species proliferate due to the nutrient preferences of different algal groups (e.g., Heisler et al. 2008; Glibert et al. 2016). Toxic and fish-killing algae are commonly associated with finfish and molluscan production (Wu et al. 1994; Honkanen and Helminen 2000; GEOHAB 2010), while high-biomass bloom-forming algae are more commonly associated with pond production (Alonso-Rodríguez and Páez-Osuna 2003; Azanza et al. 2005). Of particular concern in both shellfish and finfish mariculture is the change in forms of N associated with excretion and microbial remineralization. Between 7 and 12% of the dissolved N waste of finfish consists of urea, the remainder most often is NH_4^+ (Kaushik and Cowey 1991), and 13% of dissolved N waste from shrimp excretion and leaching of feed waste in shrimp ponds has been found to be organic N (Burford and Williams 2001). As has been well described, there is mounting evidence that chemically reduced forms of N, including urea, differentially stimulate the growth of some types of HABs or may fuel the production of algae or bacteria on which mixotrophic HABs may feed (Glibert et al. 2006, 2016; Heisler et al. 2008; Kudela et al. 2008a; Flynn et al. 2013; Glibert and Burford 2017). The relationship between alteration in nutrient composition, not just total quantity, and the development of HABs is supported by examples from freshwater, estuarine, and marine waters globally (reviewed by Heisler et al. 2008; Anderson et al. 2002; Glibert and Burkholder 2006, 2017; Glibert et al. 2016). The fact that some HAB species are disproportionately more toxic under conditions of increasing

Fig. 12.3 Three types of mariculture and the associated N and P budgets in % of the intake (food or feed intake is 100%): (a) mollusc production in raft systems; (b) finfish production in cages; (c) crustacean production in ponds. The proportion of nutrients in dissolved versus solid form depends on the digestibility of the food or feed. The larger the digestible fraction of a nutrient in the various food or feed ingredients, the larger the fraction in dissolved form.

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N:P stoichiometry, the nutrient condition often occurring in finfish and crustacean culture, raises further concerns (Granéli and Flynn 2006; Sun et al. 2011; Fu et al. 2012; Glibert and Burford 2017; Glibert and Burkholder 2017; see also Sect. 12.7). The extent to which HABs may or may not be associated with specific aquaculture operations depends on the intensity of the culture operation and the overall husbandry practices as well as the extent to which the receiving waters are retentive or well flushed (e.g., Honkanen and Helminen 2000; Glibert et al. 2005).

Although normally considered beneficial environmentally because of their large filtering capacity, and because exogenous feed is not used when raised in culture conditions, in intensive production, molluscs can also become point sources of nutrients. Because of their low assimilation efficiency, molluscs act as nutrient pumps, transforming particulate nutrients in algal biomass to dissolved and particulate detrital nutrients; fish and crustacea in intensive culture conditions similarly act as nutrient pumps, and they are also ingesting and recycling the additional nutrient source of exogenous feed (Bouwman et al. 2011). Nutrient pollution from finfish and crustacean aquaculture is higher than that from molluscan culture generally, but nutrient release from molluscs nevertheless can be locally large. Although these relationships have begun to be characterized, there is much yet to be learned regarding the pathways, processes, and rates of nutrient regeneration within aquaculture systems, including the dynamics associated with the benthos. These data are needed to more fully capture the emerging links between aquaculture and HAB proliferations in regions where such culture has grown in volume or intensity.

In terms of overfishing and the relationships with HABs, much less is understood. A basic understanding of trophic cascades suggests that as top consumers are removed, the cycling of nutrient will change, thereby altering the flow of nutrients for primary producers. Moreover, as the trend for “fishing down the food chain” continues, the relative effects of changes in nutrient regeneration by top consumers will be further altered.

12.6 Key Question 5: How Do Anthropogenic Changes in Land Use, Agricultural Use of Fertilizer, NO_x Emissions from Vehicles, and Global Changes in Land Cover Affect the Delivery of Nutrients to Coastal Waters and the Resulting Incidences of HABs?

Our knowledge of changes in land use, land cover, and the multiple changes being brought about by anthropogenic activities leading to altered delivery of nutrients to fresh and marine waters has advanced considerably [see also Chap. 4, Glibert et al. (2018)]. As nutrients change in quantity, and quality, the likelihood of HAB proliferations also changes. The success of HABs lies at the intersection of the physiological adaptations of the harmful algal species and/or strain (population), the environmental conditions, interactions 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 favourable or unfavourable manner), in turn promoting or inhibiting their growth (Glibert and Burford 2017).

Rapid progress is being made in spatially explicit modelling that is advancing our understanding of both regional and global variability in nutrients reaching the coastal zone. Among the various models being applied in regional to global estimates of nutrient export are the Spatially Referenced Regressions on Watersheds (SPARROW), Soil and Water Assessment Tool (SWAT), and Nutrient Export from Watersheds (NEWS) models. The NEWS system of models is unique in that it can be used to estimate magnitude and sources of multiple elements (N, P, C and Si) and their different forms (particulate, dissolved inorganic, and organic; Seitzinger et al. 2005). This latter system of models, based on data from more than 5000 exoreic basins, takes into account natural sources such as N₂ fixation and P weathering as well as anthropogenic sources (nonpoint inputs from fertilizer by crop type, N₂ fixation by crops, atmospheric N deposition, and manure by animal species and point sources from sewage, as estimated by human population and treatment level; Seitzinger et al. 2002, 2005, 2010; Dumont et al. 2005; Harrison et al. 2005a, b; Mayorga et al. 2010). It is these models that were applied in Key Question 1 when global patterns of *P. minimum* and nutrient export were compared. Another such approach is the Net Anthropogenic Nitrogen Input (NANI) model, first introduced by Howarth et al. (1996), that calculates N loads to watersheds as the sum of fertilizer use, N deposition, N₂ fixation, and net food and feed imports. The NANI models have been applied to many regions, most recently to estimate N fluxes from Indian watersheds (Swaney et al. 2014). The NANI models also illustrate the gaseous dry deposition of N that is much higher in urban areas and near highways due to local deposition of vehicle emissions (Howarth 2008).

Atmospheric deposition is also increasing due to many sources, among which is volatilization of NH₃ from agricultural lands and animal operations. An estimated 30% of the N deposited on these agricultural farmlands and intensive animal operations is volatilized to the atmosphere as NH₃, with most of this deposited near the site of emission (Howarth et al. 2002). Howarth (2008) reported, based on statistics that are now outdated but nonetheless illustrative (Holland et al. 1999), that on average worldwide deposition has probably doubled in the tropics and increased more than sixfold in the north temperate zone as a result of human activities. Collectively, the message from these models is the same: there is substantial export of both N and P to aquatic systems, but in general, there is a greater export of N than P (Sutton et al. 2013; Glibert et al. 2014a). Peñuelas et al. (2012) have estimated that when fertilizer use and atmospheric deposition are considered, the molar N:P ratio of that deposited on land is in the range of 44–47, while that of land plants is generally 22–30, but of even greater concern is that the N:P ratio of input to oceans is 114–370, which is 10–20 times the stoichiometric ratio of plankton characterized by Redfield (1934).

A recent model is the Integrated Model to Assess the Global Environment-Global Nutrient Model (IMAGE-GNM), which is a coupled hydrology-biogeochemistry

model (Beusen et al. 2015, 2016) that describes delivery through aquifers, riparian zones, surface runoff, and atmospheric deposition as well as point sources to streams and rivers and subsequently in-stream retention processes. Beusen et al. (2016) used IMAGE-GNM to simulate N and P transport and retention by rivers for the twentieth century accounting for the construction of major dams and reservoirs and showed that N:P ratios in water draining to the world's oceans is rapidly increasing in many parts of the world. This is probably due to the legacy of nutrient management in agriculture during the 1970s and 1980s. For example, N concentrations in many rivers do not respond to increased agricultural N use efficiency, and as a result, European water quality is threatened by rapidly increasing N:P ratios (Bouwman et al. 2017). Latecomers to big agriculture like India and China will soon face their own nutrient legacies even as the current use of fertilizers decrease (Bouwman et al. 2017).

Examples from China again highlight the relationships between anthropogenic nutrient use and HAB proliferation. China's estuaries and coasts are among the most rapidly eutrophying in the world. With a population of more than 20 M people, Shanghai alone discharges more than 200 t of N daily to adjacent waters. Pollution by N in China from the heavy use of agricultural nutrient has led to the Changjiang River now being among the highest in the world in terms of annual N load. The spatial extent of the associated hypoxic region in the East China Sea now rivals that in the Gulf of Mexico receiving discharge of the Mississippi River (Chen et al. 2007; Zhu et al. 2011). At the mouth of the Changjiang River, molar $\text{NO}_3^-:\text{PO}_4^{3-}$ values were 30–40 in the 1960s when HABs were comparatively rare in the East China Sea but rose to >250 by the late 1990s, numbering more than 100s. The scale of the HAB outbreaks has also increased, from 1000s of km^2 in 2000 to >15,000 km^2 by 2005 with many millions of dollars of lost production of fish due to hypoxia and direct toxic effects (Zhou et al. 2008; Li et al. 2009; Glibert et al. 2014a). Fertilizer N 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). More specifically, the use of N increased from 1980 to 2010 from ~0.5 to >1.2 tonnes $\text{km}^{-2} \text{ year}^{-1}$ in the Changjiang River, from ~0.1 to ~0.2 tonnes $\text{km}^{-2} \text{ year}^{-1}$ in the Yellow River, and from ~0.4 to >1.2 tonnes $\text{km}^{-2} \text{ year}^{-1}$ in the Pearl River basins (Ti and Yan 2013). In parallel with these trends in nutrient loading, the number of HABs has increased in virtually all waters of China in the past three decades. In addition to these blooms, "green tides" have increased. These noxious macroalgal blooms (*Ulva prolifera*) received notoriety during the 2008 Qingdao Sailing Olympics, when the water was blanketed with thick green scums [Hu et al. 2010; see also Chap. 16, Liu and Zhou (2018)]. More recently "brown tides" have become recurrent in the Bohai Sea [Zhang et al. 2012; see also Chap. 15, Yu et al. (2018)].

Without question, much has been learned on a global scale regarding the export of nutrients, the stoichiometric balance of that export, and the complexity of factors that alter nutrients in total load and composition as they are transported from land to the sea or to freshwaters. Models of nutrient export have greatly advanced, but there

remain many challenges. Data availability for model development and calibration for some parts of the world is very good, but for other regions, the data are poor. Improved spatial dimension of loading models is also needed. Dispersal of the nutrient and the interaction with the physical dynamics of the receiving water is still difficult to quantify. While river plume dynamics may be understood, plumes of nutrients from nonpoint sources are still largely difficult to resolve. Also, in spite of the range of examples provided here, there is much yet to be understood in terms of the role of different nutrients on toxin production. Coupling the physiological adaptations of the harmful algal species and/or strain (population), with the environmental conditions, and physical dynamics will remain a challenge.

12.7 Key Question 6: How Do the Stoichiometry and Quality of These Nutrient Sources Regulate the Biological Response, Including Toxins, Favouring HABs?

Considerable emerging evidence has shown that as nutrients change in total loads and in proportion, as already described, there are also effects on toxin production. Many cyanobacteria and marine dinoflagellate HABs have been shown to be more toxic when N is in stoichiometric excess over P, as is the case for many regions of the globe (reviewed by Glibert 2017). 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 cyanobacteria *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 lutein, 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 *P. 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* spp. (Bates et al. 1991; Pan et al. 1996; Sun et al. 2011). There are also examples of toxin production being stimulated at the opposite N:P spectrum. The freshwater cyanobacterium, *Cylindrospermopsis raciborskii*, was shown to increase the proportion of toxic strains 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 physiological “overflow metabolism” (Glibert et al. 2016; Glibert 2017).

12.8 Key Question 7: Do Climate Change and Climate Variability Have Impacts on Ecosystems that Augment the Impacts of Eutrophication and the Formation of HABs?

Nutrient changes and those of climate are complex on many levels, as has been highlighted in other chapters of this volume [see also Chap. 4, Glibert et al. (2018) and Chap. 5, Wells and Karlson (2018)] and elsewhere (e.g., Doney 2010; Fu et al. 2012; Wells et al. 2015). Climate controls many of the fundamental parameters regulating algal growth, including water temperature, nutrients, and light, 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 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. 2012, and references therein). These changes, in turn, will alter stratification, availability of nutrients and their forms and ratios, pCO₂, and light regimes among other factors (e.g., Boyd and Doney 2003), all of which control the extent to which HABs become established. Temperature affects growth rate, motility, germination, pigment content, enzyme reactions, photosynthesis, and various other processes, influencing the ability of cells to thrive in a particular area (e.g., Wells et al. 2015 and references therein). Increasing temperatures positively affect those taxa with higher temperature optima for growth and negatively influence those taxa that have lower temperature optima. Negative influences of increasing temperature can disproportionately affect diatoms, as they generally thrive in colder seasons, are more abundant in polar and temperate regions, and tend to have colder temperature optima than other microalgal groups (Harris 1986; Glibert et al. 2016, and references therein). Moreover, the uptake of NO₃⁻ and its reduction to NH₄⁺ generally decreases at higher temperatures, especially above 15–18 °C (e.g., Lomas and Glibert 1999; Glibert et al. 2016), further suggesting that diatoms, which are more typically NO₃⁻ specialists, are negatively impacted as temperatures rise. In contrast, many cyanobacterial and dinoflagellates 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 live, including bacteria, viruses, competing phytoplankton

taxa, and grazers (Wells et al. 2015 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 be associated with slower growth rates (e.g., Ogata et al. 1989; Lewis et al. 1993), but slower growth rates need not necessarily be detrimental to HAB formation if other factors, such as reduced grazing, come into play [see Chap. 7, Flynn et al. (2018)].

Examples can be found through the USA 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 may contribute to range expansion of particular species. Higher temperatures promote increased water-column stability and increased thermal stratification that, in turn, favours 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 from the water column (Visser et al. 2016 and references therein). Moreover, at higher temperatures, water can become less viscous, buoyant cyanobacteria can float faster, and conversely sinking diatoms will sink faster (e.g., O'Neil et al. 2012 and references therein). With climate change, diatoms are seemingly negatively affected in several ways.

As mentioned above, warming trends are causing changes in the C cycle, resulting in acidification of the oceans and some estuaries. This contrasts with the high pH caused by high-biomass blooms that occur due to drawdown of CO_2 . As acidification reduces pH, 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 modelling approaches, illustrated the complexity of effects of changes in pH coupled with eutrophication on phytoplankton species succession. Eutrophication increases the phytoplankton biomass that can be supported during a bloom, and the resultant uptake of dissolved inorganic C (DIC) during photosynthesis increases water-column pH. This increased pH can adversely affect plankton growth of some species, but not necessarily of others (e.g., some HABs). Using experimental analyses of the growth of three contrasting phytoplankton under different pH scenarios, coupled with mathematical models describing growth and death as functions of pH and nutrient status, Flynn et al. (2015) were able to show how different conditions of pH modify the scope for competitive interactions between phytoplankton species. Their work also suggested that, when coupled with effects on grazers, ocean acidification and eutrophication may increase the frequency of HABs, including blooms of mixotrophic species.

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 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., Miller et al. 2006; Burkholder et al. 2006; Heisler et al. 2008). As examples, within days after Hurricane Isabel in 2003 in the USA, 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 EDAB species *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. 2009b) and a similar response appears to have been initiated with the passage of Hurricane Irma in 2017.

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 North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO), can also alter conditions for HAB species. In the northern Iberian Peninsula, for example, the harmful dinoflagellate *Gymnodinium catenatum* was abundant during the mid-1980s when there was a transition from downwelling-favourable conditions to upwelling-favourable conditions, following a shift in the North Atlantic Oscillation (NAO) index (Alvarez-Salgado et al. 2003). In the 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 2014), a feature associated with the unusually strong El Niño event and the Pacific Decadal Oscillation (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 in suitable forms, to proliferate, and suitable temperatures for rapid growth. Regulatory limits of domoic acid (DA) were exceeded along the entire coast for months, and toxin impacts were felt at many levels of the food chain, 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.

The interacting effects of pCO₂, temperature, and nutrient supply complicate the interpretation of effects of pCO₂ on HAB toxicity (e.g., Boyd and Hutchins 2012; Gobler et al. 2016). High CO₂ may also affect toxicity of HABs through various routes. An overall trend of increasing toxicity with increasing pCO₂ has been reported for numerous strains of cultured *Alexandrium ostenfeldii* (Kremp et al. 2012), but culturing approaches can affect the extent to which relationships were observed between elevated pCO₂ and toxicity in some harmful algal species (Van de Waal et al. 2011). The synthesis of at least some toxins is light dependent, as is the case for karlotoxin production by *K. veneficum* and saxitoxin production by *Alexandrium catenella* (Adolf et al. 2008b), suggesting that as photosynthesis is affected by changing pCO₂, toxin synthesis is also altered. In the toxicogenic diatoms *Pseudo-nitzschia multiseriata* and *P. fraudulenta*, concentrations of their

toxin, DA, have increased at high CO₂/low pH in some studies (e.g., Sun et al. 2011; Tatters et al. 2012). This effect can be more pronounced when cells are nutrient-limited or when forms of N shift from oxidized to reduced forms (Glibert et al. 2016 and references therein).

The linkages between changes in nutrient supply to aquatic systems and climate are clearly complex. These complexities create even greater challenges for predicting how HABs may change. Using a global modelling approach, which coupled a climate change model in a coupled oceanographic-biogeochemical model, the potential effects of nutrient loading and climate change for end of the century conditions for two HAB genera, pelagic *Prorocentrum* and *Karenia*, were estimated for three regions of the globe, NW European Shelf-Baltic Sea system, NE Asia, and SE Asia (Glibert et al. 2014b). Projections for the different HABs applied a set of physiological “rules” based on suitable temperature, salinity, and nutrient conditions for growth. The nutrient conditions applied a nutrient ratio approach, rather than specific concentrations. Inasmuch as the goal was to identify the likelihood of conditions supportive of blooms, rather than their strength or magnitude, absolute concentrations were not necessary. Based on these models, an expansion in area and/or number of months annually conducive to development of these HABs along the NW European Shelf-Baltic Sea system and NE Asia was projected for both HAB genera, but no expansion (*Prorocentrum* spp.), or actual contraction in area and months conducive for blooms (*Karenia* spp.), was projected in the SE Asian domain (Glibert et al. 2014b). The implications of these projections, especially for Northern Europe, are shifts in vulnerability of coastal systems to HAB events, increased regional HAB impacts to aquaculture, increased risks to human health and ecosystems, and economic consequences of these events due to losses to fisheries and ecosystem services.

Clearly, current models provide some realizations of future states on a regional to global basis but are insufficient to address the response to HABs to the combined effects we are facing. Not only are advances needed in the coupling of land-use nutrient export models, but their coupling to oceanographic models and climate models is still in early stages of development. Considerable new data and computational capabilities will continue to be needed.

12.9 Conclusions

In sum, the evidence is unequivocal that, as concluded in the GEOHAB (2005) report on HABs in Eutrophic Systems and in the scientific consensus report by Heisler et al. (2008), HAB species can be directly and/or indirectly stimulated by nutrient over-enrichment, and nutrient enrichment interacts with other major drivers, such as hydrological changes, food web interactions, and climate change, in both direct and indirect ways as drivers of HABs. While over-enrichment of coastal waters by nutrients is a major pollution problem worldwide, it is not only total nutrient loads that promote HABs and alter microbial biodiversity. There are

still many places and times where nutrient pollution continues to be minimal, and therefore nutrients and eutrophication are not a major contributor to HABs in those locations or time, but overwhelmingly we now recognize that, indeed, there are more blooms, more often, in new and different places, often lasting longer, with a range of toxicities, and many of these blooms are related to the global increase in nutrient pollution.

Many questions remain. Indeed, there are gaps to fill in all of the key questions listed here. Much needs to be done in parameterizing rates, characterizing traits, and how they are both externally driven and internally dynamically regulated. Many species are understudied. Work needs to advance in understanding the physiological responses to excess nutrient availability and relationships with toxicity, among other physiological processes. Improved understanding of when a nutrient becomes a “stress” and how these stresses are compounded by other stresses (such as light, temperature, pH) is sorely needed (Allen and Polimene 2011; Glibert et al. 2013; Glibert 2017).

A new emphasis on improved model formulations is needed, including efforts to incorporate dynamic balance models for physiology (Glibert et al. 2013). The plasticity of nutritional pathways, as well as the plasticity of food web interactions, including grazing, allelopathy, symbioses, and other interactions, creates immense challenges for model 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. Understanding and parameterizing these relationships and how they change under our new reality of altered environmental conditions (nutrient loads, forms, temperatures, pH) have implications for modelling current and projected changes in HABs as climate and nutrient change. Further advances in linking land-use nutrient models (by amount, form, and proportion), coastal typology, climate change, regional ocean models, and biogeochemical and physiological responses are needed. Through continued and new international and multidisciplinary collaborations, such as those that may be fostered through the GlobalHAB Programme, such advancements will be possible.

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