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Harmful algae at the complex nexus of eutrophication and climate change

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ABSTRACT

Climate projections suggest–with substantial certainty–that global warming >1.5 °C will occur by mid-century (2050). Population is also projected to increase, amplifying the demands for food, fuel, water and sanitation, which, in turn, escalate nutrient pollution. Global projections of nutrient pollution, however, are less certain than those of climate as there are regionally decreasing trends projected in Europe, and stabilization of nutrient use in North America and Australia. In this review of the effects of eutrophication and climate on harmful algae, some of the complex, subtle, and non-intuitive effects and interactions on the physiology of both harmful and non-harmful taxa are emphasized. In a future ocean, non-harmful diatoms may be disproportionately stressed and mixotrophs advantaged due to changing nutrient stoichiometry and forms of nutrients, temperature, stratification and oceanic pH. Modeling is advancing, but there is much yet to be understood, in terms of physiology, biogeochemistry and trophodynamics and how both harmful and nonharmful taxa may change in an uncertain future driven by anthropogenic activities.

1. Introduction

In late October 2018, the Intergovernmental Panel on Climate Change issued a special report outlining the impacts of global warming > 1.5 °C above pre-industrial levels, which they conclude–with high confidence–is likely to occur between the years 2030 and 2052 (IPCC SR 1.5). In November 2018, the most recent US National Climate Assessment was released (Reidmiller et al., 2018), concluding that only with substantial and sustained reductions in greenhouse gas emissions can an increase in the global annual average temperature relative to preindustrial times be limited to less 2 °C, and without significant greenhouse gas mitigation, the increase in global annual average temperature could be much higher by the end of this century.

By the year 2050 human population will likely be nearly 10 billion, a 30% increase over current population estimates, with more than half of this increase expected to occur in Africa (http://www.un.org/en/ development/desa/news/population/2015-report.html). By then also, it is expected that half the population will reside in urban areas, and that megacities (>10 million people) will continue to be concentrated in China as well as other parts of Asia and Africa, most of which are along coastlines (United Nations, 2014). The demands for food, fuel, water and sanitation will only continue to rise. To support this increase in population and the required food supply, it is projected that global use of nitrogen (N) fertilizer, which has increased about 9-fold since 1970, will continue to rise, and specifically that of urea will double by the year 2050 (Heffer and Prud'homme, 2016). Phosphorus (P) use will increase also, but likely not as steeply as that of N (e.g., Sutton et al., 2013; Glibert et al., 2014a). Since 1970, P use has increased about 3-fold, leading to an upward trend in N:P fertilizer applications (Glibert et al., 2014a; Fig. 1).

There is no doubt that these changes in climate and nutrients are contributing to global eutrophication and the expanding global footprint of harmful algal blooms (HABs). There are more HABs, more often, in new and different places, in both fresh and marine waters, often lasting longer, and which have a range of impacts as well as a range of toxicities (Anderson, 1989; Hallegraeff, 1993; Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB, 1998; Smayda, 2002; Glibert and Burkholder, 2018). While there remain some lingering skeptics, and indeed there are blooms that are unrelated to nutrient pollution, the debate as to whether the global increase in HABs is a function of increasing nutrient pollution, by and large, is no longer. It is now unequivocally recognized that the global expansion of HABs is continuing, with increasing abundance, frequency, and geographic extent of HABs, with new species being documented in new areas (e.g., Anderson et al., 2002; Dale et al., 2006; Edwards et al., 2006; Heisler et al., 2008; Hallegraeff, 2010). It is also well accepted that human activities, especially nutrient pollution and climate changes, are important, if not the most important contributor(s) to this expansion (e.g., Heisler et al., 2008: Anderson, 2014: Wells et al., 2015: Taranu et al., 2015; Glibert and Burford, 2017 and references therein). Indeed, the latest climate assessment (Reidmiller et al., 2018) projects that red tides, such as those that have been relentless in Florida over the past

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Fig. 1. Conceptual figure illustrating (upper left corner and top icons), sources of nutrient pollution and the changing environmental factors with climate change, and the panels below show the trends with time in N and P fertilizer use (as tonnes) and the change in fertilizer N:P on a global scale (weight:weight). Fertilizer data reproduced from Glibert et al. (2014a) under creative commons license. The middle panels illustrate for a typical diatom, picocyanobacterium and dinoflagellate, their cell structures, yielding, as depicted in the right panels, a trajectory of change in diatoms (top panel) and cyanobacteria and dinoflagellates (lower panel).

few years will become even more frequent.

This paper examines these increasing proliferations of HABs and their intersection with globally and regionally changing nutrients and climate. Recognizing that much has been written about various aspects of these relationships (e.g., Davis et al., 2009; Fu et al., 2012; O'Neil et al., 2012; Boyd and Hutchins, 2012; Wells et al., 2015; Glibert and Burford, 2017; Glibert and Burkholder, 2018, among others), this paper focuses on several aspects not previously highlighted, while briefly summarizing more commonly accepted patterns and interactions. An underlying theme of this paper is that while we have focused on, and generally have a good understanding of, the direct effects of changing environmental variables, including, for example, nutrients, temperature, and pH on HABs, there are also more complex, subtle, and nonintuitive effects and interactions that also bear emphasizing and that add complexity to forecasts. This is not meant to be a complete review, but rather a snapshot of the complex confluence of factors at the nexus of eutrophication and climate change. Understanding how non-HAB taxa such as non-toxic diatoms may change under projected changing environmental conditions is also important if we are to understand how ecological niches may become more favorable for HAB taxa. Models, ranging from land-use and climate models, to physiological, trophodynamic, and biogeochemical constructs, are contributing to our understanding of these relationships.

2. Land-based and air-based nutrient loads

The industrial fixation of nitrogen gas (N₂) to ammonia (NH₃), the Haber Bosch process, N₂ + $3H_2 -> 2$ NH₃, is considered to be one of the most important chemical reactions in the world (e.g., Smil, 2001) and "the greatest single experiment in global geo-engineering ever made" (Sutton et al., 2013, p. 4). This reaction has produced the N fertilizers that have contributed to the 'green revolution' responsible for increased food production that has supported the expansion of human population from ~2 billion in the early 20th century to >7 billion people today (Smil, 1999; Erisman et al., 2008). The upward trends in N and P fertilizer application are apparent in virtually all regions of the globe. In the US, it has been estimated that there has been at least a 5-fold increase in reactive N use on average compared to pre-industrial time (Houlton et al., 2013), but this increase is spatially variable ranging from negligible to 35-fold in different areas (Sobota et al., 2013).

Through use of spatially explicit modeling efforts, including the Global Nutrient Export from WaterSheds (Global NEWS; Seitzinger et al., 2005, 2010; Dumont et al., 2005; Harrison et al., 2005a,b), and next-generation models, such as the Integrated Model to Assess the Global Environment-Global Nutrient Model (IMAGE-GNM; Beusen et al., 2015, 2016), the large differences in nutrient use between regions, and over time, have been documented, as well as differences in nutrient export by element. These models have shown that throughout much of Asia, western Europe and eastern North America, fertilizer and manure together constitute the largest source of inorganic N (DIN) export at the mouth of rivers (Dumont et al., 2005); agricultural sources of DIN (which include fertilizer, animal manures and agricultural N2 fixation) collectively contribute about half of the total DIN exported globally (Dumont et al., 2005). On the other hand, for dissolved inorganic P (DIP), human sewage is the largest anthropogenic source throughout much of the world, and inorganic P fertilizers and manures are less significant (Harrison et al., 2005a, 2010).

While food production and fuel consumption are most often linked with eutrophication trajectories, non-food commodities, such as clothing, goods for shelter and manufactured products can account for as much as 35% of global marine eutrophication and 38% of global freshwater eutrophication (Hamilton et al., 2018). Production of crops, such as cotton, are not normally tabulated in agricultural fertilizer use statistics, but may be significant. Fertilizer applied to cotton crops in the US for the past several decades (1995–2010) has been nearly 3-fold higher than that applied to soybeans and about 40% that applied to corn (https://lib.dr.iastate.edu/cgi/viewcontent.cgi?article = 1554& context = card_workingpapers).

Only 10–30% of agriculturally used N and P actually reaches human consumers in the intended food products (Galloway et al., 2002; Houlton et al., 2013), and more than half is lost to the environment in direct runoff and atmospheric volatilization/eventual deposition (Galloway et al., 2014). In the case of N, a single molecule of fixed N can have multiple impacts on water, air, and soil ecosystems (Galloway and Cowling, 2002). Thus, accompanying this agricultural intensification has been an acceleration of the global N cycle, a trend projected to intensify further in coming decades (e.g., Smil, 2001; Glibert et al., 2006, 2014a; Beusen et al., 2015, 2016; Bouwman et al., 2009, 2017). In countries such as China where the rate of fertilization has risen rapidly, the rate of soil retention of the excess N is actually declining (Cui et al., 2013), leading to further environmental leakage of agricultural nutrients.

Animal production has been increasing to meet the increasing demands for meat (e.g., Howarth, 2008), and animal waste, including that associated with expanding aquaculture enterprises, can be a major source of nutrient pollution (e.g., Bouwman et al., 2011, 2013a, 2013b; Glibert et al., 2018; Glibert and Burkholder, 2018). Using data for the period 1950--2010 (derived from the database FISHSTAT, FAO, 2012, 2016), simple nutrient budget models were developed to describe the major flows of nutrients in shellfish and fish aquaculture systems (Bouwman et al., 2011, 2013a). These models account for annual production, by species, country, sea and type of environment. These aquaculture models underscore that the concern for both shellfish and finfish expansion with respect to HABs is two-fold. First, there is an overall increase in nutrient concentrations with these operations, and second, there is a change in form of nutrients as a result of excretion and associated microbial remineralization (Bouwman et al., 2011, 2013a,2013b). Toxic and fish-killing algae are commonly associated with finfish and molluscan production (Honkanen and Helminen, 2000; Wang et al., 2008), while high biomass bloom-forming algae are more commonly associated with pond production (Alonso-Rodríguez and Páez-Osuna, 2003; Wang et al., 2008). Relationships between increasing prevalence of HABs and aquaculture operations are increasingly reported with associated economic impacts (GEOHAB, 2010). In China, for example, about US\$2.5 million in finfish revenues were lost in 2005 due to one single HAB event (Li et al., 2009). Single HAB fishkill events in Korea have been estimated to have cost from US\$1 to 100 million in lost fish, while in Japan such events have been estimated to have resulted in losses of fish worth more than US\$300 million (GEOHAB, 2010 and references therein).

In addition to runoff and animal wastes, atmospheric deposition of N is not only high, but increasing in many regions, particularly in the downwind plumes from major cities (e.g., Howarth, 2006; Galloway et al., 2008; Duce et al., 2008) and in the downwind plumes of major animal operations (e.g., Whitall et al., 2003). Older estimates for both European and US coastal waters suggested that anthropogenic atmospheric N deposition contributes from 10 to 40% of new N loading (Jaworski et al., 1997). The volatilization of animal wastes and manures contributes to atmospheric deposition of NH4⁺, which has been shown to account for approximately half of the atmospheric N deposition in Mid-Atlantic estuaries such as the Neuse River Estuary and Atlantic coastal waters (Paerl, 1997; Whitall et al., 2003). Recent modeling has shown that there has been a 3-fold increase in soluble N deposition over land, and 2-fold increase over the ocean due to human activities since 1850 and furthermore, while NOx emissions may decline by 20%, those of NH₃ are expected to increase by 22% by 2050 (Kanakidou et al., 2016). It has been estimated that the atmospheric deposition of nutrients in the ocean is now ~20-fold greater than the Redfield ratio for N:P (Jickells, 2006; Peñuelas et al., 2012) and these changes are also having large consequences for N:P stoichiometry in lakes (Elser et al., 2009).

From land-based use of N and P to atmospheric deposition, the proportions of N and P reaching aquatic systems from human activities are clearly changing. As emphasized throughout this review, changes in stoichiometry have important implications for HABs. Alterations in the composition of nutrient loads have been correlated with shifts from diatom-dominated to flagellated-dominated algal assemblages in many regions. For example, in the Huanghai Sea region of China, inorganic N:P ratios are now about twice Redfield proportions, and about 4-fold higher than in the 1990s (Ning et al., 2009; Glibert et al., 2014a) and there has been a corresponding nearly 6-fold increase in HAB occurrences and a shift to proportionately more dinoflagellates in comparison to diatoms (Fu et al., 2012; Glibert et al., 2014a). Similarly, in the South China Sea region, water-column inorganic N:P ratios increased from ~2 in the mid-1980s to >20 in the early 2000s (Ning et al., 2009). In addition to the increase in number of HABs, a shift in species composition to increasing dominance of genera such as *Chattonella, Karenia*, and *Dinophysis* has occurred (Wang et al., 2008). In the North Sea, as increasing N relative to P proportions developed in response to disproportionate nutrient reductions, mixotrophic dinoflagellates have been shown to have increased, and many of these are harmful species (Burson et al., 2016).

3. Nutrient export, nutrient retention

The magnitude and effect of land-based and atmospheric-based nutrient pollution on HAB proliferation depends not only on how much is exported but also how much is retained within the receiving waters. 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 is leading to the supply of the right nutrients at the right time that helps to create conditions conducive to specific HABs (Fig. 1). Hydrographically retentive zones are important for HABs, especially those that form cysts, as the cysts accumulate and can lead to blooms whenever favorable conditions occur. Of the nutrient inputs that enter most coastal systems, an estimated 22% of the riverine N and 24% of the riverine P is retained (Laruelle, 2009; Glibert et al., 2018). Estuaries in temperate regions of the Northern hemisphere are particularly important as sinks for nutrients because of the prominence of relatively long residence time tidal systems. Fjords are particularly effective in retaining nutrients with residence times as long as decades, while small deltas have a low filtering capacity. Shallow, enclosed coastal lagoons can be subject to recurrent blooms once a population of HAB taxa becomes established. In tropical and sub-tropical regions, retention can be much less efficient and a large proportion of the nutrient inputs to the ocean bypasses the coastal filter and is discharged directly onto the shelves in large river plumes (McKee et al., 2004).

In addition to effects of natural coastal typology and coastal features on nutrient retention and export, nutrient transport to downstream receiving waters is also affected by anthropogenic alteration of river discharge. Retention of nutrients in lakes increased >60% between 1900 and 2000 due to reservoir construction and other anthropogenic flow alterations (Beusen et al., 2016). Dam and reservoir construction and other in-river consumptive uses, as well as channelization of flow, have greatly modified the timing, magnitude, form, and stoichiometry of nutrient delivery to the coast. This is because P is retained more efficiently than N during processing and transport in soils, groundwater, riparian zones and streams, rivers, lakes and reservoirs (Beusen et al., 2016). It has been estimated that by 2030, 93% of all rivers will be affected by dams (Grill et al., 2015). Thousands of dams of a capacity of more than 1 MW (megawatts) were constructed during a first construction boom in the 1950s and 1960s, and a second boom is now underway, mostly in developing countries (Grill et al., 2015; Zarfl et al., 2015). For the major global dams, reactive P (total dissolved P + reactive particulate P) is the most efficiently reduced (by 43%), followed by reactive Si (dissolved Si + reactive particulate Si) (by 21%), and then total N (12%) (Maavara et al., 2014, 2015; Maavara, 2017). The result is an increase in the N:P and N:Si ratios of riverine delivery to coastal areas following dam construction. 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 favoring HABs in East China Sea (e.g., Zhang et al., 2015). In addition to the reductions in overall river flow that occurs from dam construction, large river systems can become fragmented preventing



Fig. 2. Statistics on fertilizer use by state in US. Panels a and b give the total N and P used as fertilizer and manure (1000 kg), respectively, panel c, the ratio of N:P use (by weight), and panels d and e give the percent change in N and P use, respectively, in the time period from 2007 to 2011 relative to the time period of 2002 to 2006 (www.epa.gov/nutrient-policy-data/commercial-fertilizer-purchased).

free movement of organisms, and severe modification of river flow alters temperature regimes, dramatically reduces sediment transport and alters light regimes (Vörösmarty et al., 2010; Lehner et al., 2011; Liermann et al., 2012). Much work has been done in understanding these complex hydrological properties and how to capture their features in models. In order to estimate estuarine retention of N and P globally, a coastal typological classification was developed, and a set of generic biogeochemical box models was applied for each coastal type to estimate the estuarine retention of N and P from rivers at the global scale (Laruelle, 2009; Dürr et al., 2011). The modeled retention of N and P for individual boxes compares reasonably well to data for local studies.

The effect of nutrient delivery from land to lakes, reservoirs, and coastal waters is also a function of the physics of those waters. From features such as eddies that concentrate plankton (Nishimoto and Washburn, 2002), to small-scale turbulence and stratification, physical properties play important roles in bloom aggregation. Coastal features such as banks, canyons or islands have influences on upwelling and its local spatial effects (e.g., Pitcher et al., 2010). HABs often occur in such systems when highly stratified, in some cases at the very smallest of scales. Subsurface layers of HABs have often been reported in highly stratified waters, wherein the HAB cells accumulate at the intersection of light and nutrients. Thin layers, in some cases only centimeters to meters thick, can be sites of dense HAB aggregations. Bjørsen and Nielsen (1991) described a 'magic carpet' of *Gyrodinium aureolum*, while Gentien et al. (1995) noted that some thin layers have up to 100% dominance of dinoflagellates.

The result of the greater expansion in use of N fertilizers relative to those of P, more aggressive reduction of P from sewage effluent and from laundry products, and the greater retention of P and Si by dams and in-water processing compared to N, is a global distortion of the ratios of nutrient loads (Sutton et al., 2013; Glibert et al., 2014a, 2018). The success of HABs lies at the intersection of the physiological adaptations of the harmful algal species and/or strain (population), the environmental conditions, including the right nutrient proportions, interaction with co-occurring organisms (both biogeochemically and trophodynamically), and physical dynamics that alter abiotic conditions in a favorable or unfavorable manner), in turn promoting or inhibiting their growth (Glibert and Burford, 2017).

4. A complex nexus

While the (IPCC, 2018) and the US National Climate Assessments (Reidmiller et al., 2018) can conclude, through the use of multiple model constructs, that substantial warming will occur by 2050, trajectories of nutrient change are far less certain. Not only are there uncertainties with climate models, and each model has its own inherent bias or uncertainty, the uncertainty with scenarios is much greater (e.g., Freer et al., 2018), and that with respect to nutrients highly uncertain. Future projections of eutrophication were made using a suite of assumptions in the Millennium Ecosystem Assessment (MA). Four different scenarios were developed, based on storylines developed by the IPCC and translated into changes of the main anthropogenic drivers, i.e., demography, economic development, and agricultural production (Alcamo et al., 2006). Each of these scenarios differed in their global vs regional, and their proactive vs reactive, environmental management perspectives, but all scenarios show that by 2050, major increases in N and P river export to coastal ecosystems can be expected, particularly in

South and Eastern Asia, and in many countries in South America and Africa (Glibert et al., 2018). In order to guarantee food security for populations in developing countries, and to prevent land degradation or restore soil fertility, fertilizer use will have to increase in these parts of the world. As a consequence, nutrient losses by leaching, volatilization and runoff will inevitably increase. At the same time, urbanization and lagging sewage connection and treatment of wastewater will lead to increasing nutrient discharge to surface water in developing countries. Thus, for 2050, it is projected that the HAB risk will spread in South America and Africa, will increase in East Asia where there is already high risk, but may decrease in parts of the world if higher efficiencies in agricultural fertilizer use and improved wastewater management are achieved, as projected in areas with proactive, regionally-based environmental actions (Glibert et al., 2018).

While it may seem, and has been the case over the past several decades, that the trend in nutrient use and nutrient export to aquatic systems has been ever increasing, there are signs that nutrient pollution may be slowing in some regions. Important decreasing trends are projected in Europe, and stabilization in North America and Australia. Regional nutrient reductions, the purview of local management decisions, are the most variable. It has been since the mid 1980s and 1990s that the major industrialized nations began curtailing P use by removing it from detergents and by upgrading sewage treatment processes which generally are more efficient in removing P than N (Litke, 1999; Van Drecht et al., 2009). In the US, where fertilizer and manure use is tracked by state, it can be seen that not only is there wide variation in the proportional use of N and P by state, but more states than not have reduced fertilizer use in the time period from 2007 to 2011 relative to the time period of 2002 to 2006 (www.epa.gov/nutrientpolicy-data/commercial-fertilizer-purchased; Fig. 2). More states have undertaken P control than N control, and while several states have increased use of both N or P. more have increased use of N relative to P. There is also evidence that China, where massive blooms have occurred in recent decades in both marine and freshwaters (reviewed by Glibert et al., 2014a), is investing substantially in environmental issues, including nutrient reduction measures. The extent to which these reductions will be realized in the future remains in the realm of speculation, but given the aforementioned change in patterns of fertilizer use and trends in nutrient reductions, stoichiometry of runoff is expected to continue to change, leading to further upward trends in N:P in many receiving waters (e.g., Glibert et al., 2013, 2014a, Sutton et al., 2013; Bouwman et al., 2017).

The effect that changing stoichiometry has on HABs is an important factor to consider in evaluating how HABs may change in a future ocean. In understanding of the intersection of effects of changing temperatures and nutrients, applications of key principles of ecological stoichiometry (e.g., Sterner and Elser, 2002) and metabolic ecology (e.g., Brown et al., 2004; Sibly et al., 2012) have helped in structuring conceptual ideas. With these principles, the focus is on associated changes in the traits of growth, respiration, body size, and nutrient stoichiometry (Cross et al., 2015). Building on these principles, Meunier et al. (2017) predict that increasing N:P ratios in ecosystems should shift communities toward systems with trait dominance of higher optimal N:P ratios, higher P affinity, decreasing N retention and increasing P storage. These are many HAB traits. Even with consideration of these traits and individual responses, and the associated unifying theories, the unknowns of our 'ever changing world' make projections exceeding complex-especially with respect to HABs.

5. A warmer, more extreme climate

5.1. Temperature

Changes in temperature certainly affect the habitat for HABs. Increasing temperatures should positively affect those taxa with higher temperature optima for growth, while conversely negatively influencing those taxa that have lower temperature optima. Diatoms are among those taxa with typically lower temperature optima, and have long been described as "coldwater flora" (e.g., Reynolds, 1984; DeNicola, 1996; Anderson, 2000). In contrast, many cyanobacterial and dinoflagellates species, including HAB species, prefer warmer temperature conditions (e.g. Paerl and Huisman, 2008; Paerl and Scott, 2010). Not all species naturally occur in their temperature optima, however, as growth is a function of the ensemble of environmental factors. Temperatures also affect the community of organisms within which the harmful algal species may live, including bacteria, viruses, competing phytoplankton taxa, and grazers (Wells et al., 2015 and references therein). The toxicity of many harmful algal taxa also increases with warming (Davis et al., 2009; Fu et al., 2012 and references therein).

Temperature has also been shown to alter the chemical composition of organisms. In a meta-analysis, Yvon-Durocher et al. (2015) attributed a consistent rise in algal N:P and C:P ratios with warming to be a function of the reduction in cellular P. Similarly, enhanced levels of CO_2 may also alter cellular chemical composition, leading to a rise in C:nutrient ratios of phytoplankton (Urabe et al., 2003; Schoo et al., 2013). Such increases alter trophic efficiency, food quality, and ultimately food webs (e.g., Sterner and Elser, 2002; Van de Waal et al., 2010; Schoo et al., 2013). For example, higher C:nutrient stoichiometry of phytoplankton is considered to be inferior in food quality for zooplankton (De Senerpont Domis et al., 2014). Fu et al. (2007) compared cellular C and N contents of *Heterosigma akashiwo* and *Prorocentrum minimum* under different CO_2 and temperature conditions, and while cellular stoichiometry of the raphidophyte was affected, that of the dinoflagellate was not.

Warmer waters are thought to favor smaller-sized cells as they may more efficiently harvest light and nutrients and maintain their position in the euphotic zone (Winder et al., 2009; Daufresne et al., 2009; Finkel et al., 2010). Indeed, in the oceans, small cells dominate in warm, nutrient poor waters, and larger cells are more commonly associated with cool, more nutrient rich waters (e.g., Chisholm, 1992; Maranón et al., 2012). Shifts to smaller cells have been predicted from experimental studies of Sommer et al. (2015) and Moran et al. (2010) and those of Yvon-Durocher et al. (2010). Warmer temperatures should lead to reduced elemental demands for N and P, due to the reduced demand for proteins and RNA, and with that may come a decrease in cell size (Woods et al., 2003). In past climate change events, diatoms have undergone size change events, with smaller cells consistently associated with periods of warming (e.g., Falkowski and Oliver, 2007; Finkel et al., 2007). More recently, the Great Lakes has been witnessing a shift to smaller cells associated with warming and increased stratification (Bramburger et al., 2017). In the work of Peter and Sommer (2013), however, it was shown that the effect of temperature on cell size is mediated by nutrient limitation; the slopes of the temperature-size relationship became more negative the more stringent the nutrient stress and at the lowest nutrient stress imposed, cell sizes were not significantly changed with temperature.

5.2. Stratification

Among the stressors associated with warmer waters is a change in density gradients and increased stratification (e.g., Dale et al., 2006; O'Neil et al., 2012). Higher temperatures promote increased watercolumn stability which has the dual effect of increased sinking rates for larger-sized taxa and decreased nutrient flux from deeper waters (e.g., Winder et al., 2009). Increased thermal stratification favors known bloom-forming, toxigenic cyanobacterial species that control their vertical position through internal buoyancy regulation or that are diazotrophic (e.g., Walsby, 1975; O'Neil et al., 2012; Visser et al., 2016 and references therein). In marine waters this increased stratification may also favor flagellates that can swim to obtain their requisite nutrients from deeper waters, or that can obtain their nutrients through acquisition of particulates (e.g., Dale et al., 2006; Stoecker et al., 2017; Selosse et al., 2017).

There are also light effects projected to occur in a warming world, and cell size and community structure will again be affected. With increased stratification and mixed-layer shallowing, those cells that are less susceptible to photoinhibition may be favored (Finkel et al., 2010). Again, smaller cells have the advantage, as they generally have larger cross sectional area for photochemistry, but faster repair of photodamage (Key et al., 2010). This effect is synergistic with temperature. Cells increase light harvesting pigment content as downstream photochemistry increases (with temperature), but, in turn this increases the package effect (Kirk, 1994; Beardall et al., 2009a). Small cells overcome this effect.

5.3. Precipitation, storm frequency, drought

Climate changes may further influence harmful algal species expansions due to altered precipitation patterns, including increases in droughts in some regions, and/or increased frequency or intensity of storm events in other regions (e.g., Heisler et al., 2008; O'Neil et al., 2012). 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). Extreme heat and precipitation events have been on the rise in recent decades and are projected to increase in frequency and intensity in future decades, according to the recent IPCC report (2014) and the most recent US national climate assessment (Reidmiller et al., 2018). In an early review of climate change around the globe, Easterling et al. (2000) noted that changes in total precipitation were amplified at the extremes, and that changes in average temperature were accompanied by more temperature extremes. Using historical observations and a large climate model ensemble, Diffenbaugh et al. (2018) quantified the influence of global warming on extreme heat and precipitation events around the world, and found that the historical climate forcing increased the probability of wettest 5-day periods by 41% globally. These high precipitation event statistics include flooding due to strong storms, as exemplified in 2017 when numerous tropical storms and hurricanes impacted the Gulf of Mexico and Caribbean waters, with peak impact during the fall season.

Hurricane Florence (September 2018) represents one such example, with an amount of water equal to the volume of Chesapeake Bay delivered as rainfall to the states of North and South Carolina (Meyer, Sept 14, 2018). Undoubtedly, these extreme precipitation and flooding events alter the coastal habitat and may create conditions more conducive to HABs through the massive associated quantities of runoff, as nutrient supply is tightly coupled with freshwater input (e.g. Caraco, 1995; Vitousek et al., 1997) that, in turn, is driven by regional climate variability (Najjar, 1999; Miller et al., 2005; Burkholder et al., 2006; Paerl et al., 2006; Schulte et al., 2016). The combination of more freshwater input and warmer temperatures has been found to enhance the probability of, and habitat for, at least some types of HABs (e.g., Paerl and Huisman, 2008; O'Neil et al., 2012; Wells et al., 2015).

Climate changes are expected to change seasonality, with longer springs and falls as well as hotter summers in some areas. Springs in Chesapeake Bay are expected to become wetter, and it is projected that this will increase N loads–even in the absence of increases in land-based applications; an increase in N flux down the Susquehanna River (the major tributary of Chesapeake Bay) of 17% by 2030 and 65% by 2095 is expected from flow changes alone (Howarth, 2008). Based on climate downscaling models for the Chesapeake Bay region, projected for the years 2041–2070, these N loads will not only increase in spring, but DIN:DIP will also increase substantially, increasing the potential habitat for species such as *Prorocentrum minimum*, which typically occur in spring under such skewed inorganic nutrient proportions (Tango et al., 2005; Glibert et al., 2012). after, and in some cases, being maintained long after, hurricanes and their associated precipitation (e.g., Tester et al., 1999; Burkholder et al., 2004; Miller et al., 2005; Havens et al., 2016). Within days after Hurricane Isabel in 2003, a large phytoplankton bloom developed in Chesapeake Bay, linked to increased nutrient loads (Miller et al., 2005). A bloom of the picocyanobacterium Synechococcus in eastern Florida Bay, lasting more than 18 months, followed an injection of nutrients from the high freshwater discharge caused by Hurricanes Katrina, Rita and Wilma in 2005 (Glibert et al., 2009a). Also in Florida, releases of Lake Okeechobee water to the lagoons on Florida's east coast were accelerated in summers 2016, 2017, and 2018 due to heavy rains, and the nutrient pollution carried with these flows resulted in what was termed a 'guacamole-thick' bloom of cvanobacteria, mostly Microcvstis (Mettler, 2016). In 2018, the west coast of Florida experienced the largest and most persistent Karenia brevis bloom in nearly 10 years, lasting more than a year, leaving a wake of devastation in wildlife deaths, human health issues, and economic impacts (Wei Haas and Depp, Aug. 8, 2018; Visser, Aug. 15, 2018). There is considerable evidence that the severity of the 2018 K. brevis bloom was related to the intense flooding and runoff that occurred following Hurricane Irma in fall 2017. This bloom appears to have been sustained by the unrelenting wet weather that continued through mid 2018 and that led to saturated ground and overflowing lakes, rivers and streams (Fritz, 2018). With the runoff from Hurricane Irma, the bloom was likely fueled with an injection of nutrients allowing the K. brevis cells, which normally begin their growth offshore, to grow in abundance. In summer 2018, this bloom moved inshore where it encountered additional sources of nutrients that have sustained it and, together with summer warm waters, growth was further promoted. Of those additional sources of nutrients may be increased nutrient-laden flow from the Caloosahatchee River, linked to the same discharges of Lake Okeechobee as those thought to support the Microcystis bloom mentioned above. The last such massive K. brevis bloom occurred in 2005-2006, lasting over 16 months, and again, appeared to have been initially fueled by the many hurricanes that passed through and over Florida that year.

In coastal lagoons where riverine input is not the dominant source of nutrient delivery, climate variability can alter the input of groundwater nutrients (e.g., LaRoche et al., 1997). Long-term changes in, or intensification of, climate forces such as monsoons or inter-annual 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-favorable conditions to upwelling-favorable conditions, following a shift in the North Atlantic Oscillation (NAO) index (Alvarez-Salgado et al., 2003). In late 2013, and continuing through much of 2016, anomalously warm water developed in the northeastern Pacific Ocean (e.g., Bond et al., 2015; Freeland and Whitney, 2014), a feature associated with the unusually strong El Niño event and the PDO). The warm water moved over the continental margin, eventually extending from southern California to Alaska by spring 2015. Coupled with seasonal upwelling, conditions were ideal for Pseudo-nitzschia that had sufficient nutrients, and the right nutrients, to proliferate and suitable temperatures for rapid growth. Regulatory limits of domoic acid were exceeded along the entire coast for months, and toxin impacts were 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 (Smith et al., 2018).

Responses to changing precipitation events are far from certain, however. Greater salinity fluctuations, such as those that estuaries are experiencing with changing precipitation may favor halotolerant and euryhaline species (e.g., Fu et al., 2012). Many species of *Prorocentrum*

fit this descriptor, as shown for *P. lima* in which both growth and toxicity were found to be inversely related to salinity (Morton et al., 1994). In *Karlodinium veneficum*, low salinity reduced growth rates but increased cellular toxicity (Adolf et al., 2009). Similarly, *Karenia brevis* may be more toxic under reduced salinities (Errera and Campbell, 2011). There is much variability in such responses, however, and *Pseudo-nitzschia multiseries*, in fact, has shown the opposite pattern (Doucette et al., 2008).

While extreme storms and precipitation events have been linked directly and indirectly to many HAB events, drought and its consequence, wildfires, may also be related to runoff and nutrient enrichment. Wildfires may be increasing, and the 2017–2018 wildfires in the western US were extensive, and it has been estimated that due to the estimated fewer days of snowpack in much of the west, longer and more intense fire seasons can be expected in coming decades (https://www.outsideonline.com/2289216/20-years-wildfires-will-be-six-times-

larger; Reidmiller et al., 2018). Climate is also changing the timing of the rainy season, as exemplified by California which has experienced delayed rainy seasons and more fires in recent years. Fire changes the properties of soil, allowing for more runoff when it does rain. Depending on terrain, runoff in the year following a fire can increase as much as 30%, and loss of vegetation further leads to erosion (Paige and Zygmunt, 2013). Fire also increases the availability of soil nutrients through combustion and accelerated decomposition processes. Moreover, many fire retardants used in fighting fires are NH₃ and P-containing compounds. California applied over 5.5×10^7 liters of retardants in 2017, and in 2016, the US Forest Service applied 7×10^7 L on National Forest systems across the country (https://www.kqed.org/science/1917995/fire-retardant-use-explodes-as-worries-about-water-wildlife-grow).

5.4. Complicated biogeochemistry

Warming trends are causing massive changes in the carbon (C) cycle, with large associated effects on pH and thus changes occurring in aquatic C chemistry due to accelerating levels of atmospheric CO2 are expected to affect organisms that are pH-sensitive. Increasing levels of CO₂ may also favor algae that depend on diffusive CO₂ rather than HCO_3^{-} as their C source or those that may downregulate their carbon concentrating mechanisms (CCMs) and therefore reallocate energy to different pathways (Raven et al., 2005; Rost et al., 2008; Beardall et al., 2009b; see also Raven et al., 2019). This latter description includes many harmful algal species, such as Amphidium carterae and Heterocapsa oceanica (Dason et al., 2004), but this is not the case for all HABs. Shifts in pH due to increased CO2 may also alter habitat for HABs. As pH declines, there is some evidence that cyanobacteria can out-compete eukaryotic algae; laboratory studies suggest that some cyanobacteria increase growth rates under such conditions (O'Neil et al., 2012 and references therein). In highly productive, high-biomass systems, pH values vary substantially over diel periods or over the life span of a bloom. In such systems, the pH trajectory is often one of increase, rather than decrease, which is the dominant direction of change occurring due to increased CO_2 and climate change; pH values >9 commonly occur during dense blooms (Shapiro, 1997; Jacoby et al., 2000; López-Archilla et al., 2004; Glibert et al., 2011; Gao et al., 2012a; Yang et al., 2017). These dynamic pH swings create different challenges for organisms than do the acidification effects of acid deposition and climate change that affect oligotrophic waters (e.g. large oligotrophic lakes and pelagic ocean waters). Such elevated pH may, in turn, alter bacterial metabolism and may also affect the biogeochemical cycling of N, including the chemistry of NH₄⁺ - NH₃ and processes such as nitrification, denitrification, and dissimilatory NO₃⁻ reduction to NH₄⁺ (DNRA) as well as the efflux of P from the sediment (Seitzinger, 1991; Kemp et al., 2005; Tank et al., 2009; Glibert et al., 2011; Gao et al., 2012a; 2012b).

also contingent upon the nutrient conditions, as the size spectra of individuals typically increases in nutrient-enriched ecosystems (e.g., Sprules and Munawar, 1986; Irwin et al., 2006). But projections of changes in cell size are not that simple. In a study of varying effects of CO_2 on diatoms of varying diameters, Wu et al. (2014) found that the larger cells were disproportionately stimulated, a finding confirmed by Tortell et al. (2008) who also observed a shift to larger diatoms cells (from small penates to large chain-forming centrics) as CO_2 increased.

Flynn et al. (2015), in a series of experiments coupled with modeling approaches, illustrated the complexity of effects of ocean acidification and eutrophication (or de-eutrophication) on phytoplankton species succession. Using three species, a weakly calcifying strain of the non-motile prymnesiophyte (*Emiliania huxlevi*), a motile cryptophyte (Rhodomonas sp.), and a silicifying diatom (Thalassiosira weissflogii), cultures were grown in present day pH conditions (8.2), more acidic, future pH conditions (7.6), and conditions that were more basic, representative of a dense bloom (8.8). They also compared cultures wherein pH was allowed to drift from initial conditions, and those where initial conditions were maintained through acid or base additions. Growth of Thalassiosira and Emiliania was almost halved in the basic cultures where pH was allowed to drift, but their growth was similar or slightly enhanced in the acidic-drift systems. There was little difference between Rhodomonas grown in drift systems of different initial pH, at least during the nutrient-replete phase. They coupled these results with models, and when emergent relationships were compared for pairs of species, potential windows of opportunity for each competing species became apparent. Emiliania growth was favoured under extant pH, with more acidic and basic conditions being unfavourable. Rhodomonas, which had the lowest maximum growth rate, had its highest competitive scope at elevated pH but only when nutrient-replete; these are conditions likely associated with eutrophic areas during blooms. Rhodomonas and other cryptophytes may serve as food for mixotrophic HABs and thus as the scope for their expansion increases. some HABs may be favored (see also Section 7). Their work also suggested that, when coupled with effects on grazers, ocean acidification and eutrophication will increase the frequency of HABs, including blooms of mixotrophic species.

The interacting effects of pCO₂, temperature, and nutrient supply also complicate the interpretation of effects of pCO₂ on HAB toxicity (e.g., Boyd and Hutchins, 2012; Gobler et al., 2016). The literature is at best conflicting with regard to CO₂ and pH effects on HAB toxicity. Much of this has to do with differing methodologies between studies (Fu et al., 2012; Finkel et al., 2010; Van de Waal et al., 2011). As an example, Lundholm et al. (2004) and Trimborn et al. (2009) found that *Pseudo-nitzschia* increased toxicity at higher pH, while Sun et al. (2011) and Tatters et al. (2012) found that toxin levels increased under higher CO₂ levels. High CO₂ may affect toxicity of HABs through various routes. The synthesis of at least some toxins is light dependent, as is the case for karlotoxin production by *Karlodinium veneficum* and saxitoxin production by *Alexandrium catenalla* (Proctor et al., 1975; Adolf et al., 2008), suggesting that as photosynthesis is affected by changing pCO₂, toxin synthesis may also be altered.

6. Diatoms may be disproportionately stressed

Most efforts to describe the impacts of eutrophication and climate change–individually or collectively–on HABs, have focused on the HAB species (e.g., Davis et al., 2009; Fu et al., 2012; O'Neil et al., 2012; Boyd and Hutchins, 2012; Wells et al., 2015; Glibert and Burford, 2017; Glibert and Burkholder, 2018, among others). It is also appropriate to examine the effects on non-HAB diatoms and why their competitiveness may change. Several factors are considered here. If non-HAB diatoms are less likely to be competitors, non-diatom HABs may have the potential to become more prevalent, even in the absence of specific favorable adaptations.

Diatoms often thrive in colder seasons, are more abundant in polar



Fig. 3. Examples from mesocosm studies showing the change in phytoplankton composition when enriched with different nutrients. Panels a and b show the change in accessory pigment composition (Y axis) relative to total chlorophyll a (X axis) for mesocosms with water from Florida Bay enriched with equimolar concentrations of NO₃⁻ (panel a) and NH₄⁺ (panel b). The treatment shown in panel a also received an addition of PO₄³⁻. Note that under $NO_3^- + PO_4^{3-}$ enrichments, diatoms (as fucoxanthin) increased, whereas peridinincontaining dinoflagellates did not. With NH4+ enrichment, cyanobacteria (as zeaxanthin) increased, while cryptophytes (as alloxanthin) decreased. From Shangguan et al. (2017) and reproduced with permission of the publisher). The lower panel, c, depicts the long-term change in phytoplankton response to NH4+ amendments in bioassays from Wascana Lake, Canada. Note that in the early years of the study, NH4+ served as a stimulant of spring production, whereas in the more recent years, it has been a suppressant. From Swarbrick et al. (2019) reproduced under creative commons license).

and temperate regions, and tend to have colder temperature optima than other microalgal groups. Diatoms, being generally considered an "r" selected group, would be expected to have a low N:P ratio and thus would be expected to be outcompeted if N:P in the environment increases (e.g., Mitra et al., 2014). Diatoms also have an obligate requirement for dissolved Si (DSi), and asymmetric changes in N relative to DSi resulting from DSi retention restrict their supply of this required element. What is less well appreciated is that diatom composition may also change with eutrophication and changes in nutrient stoichiometry. In the Yellow Sea, for example, in association with a decline in loads of DSi but increases in N, there has been a seemingly counterintuitive change to more heavily silicified diatoms in winter (Liu and Glibert, 2018). It is thought that sequestration of Si in valves of these heavily silicified diatoms has the biogeochemical consequence of a weakening of the Si pump and a slowing of biogenic Si dissolution, thereby reducing availability of Si for further diatom growth in subsequent seasons and increasing the window of opportunity for summer growth of nondiatom HAB taxa (Liu and Glibert, 2018).

In a rising CO₂ world, diatoms may also be disfavored in the competition with those cells that lack C concentrating mechanisms (CCMs, e.g., Riesbesell, 2004; Fu et al., 2012; King et al., 2015). Diatoms have highly efficient CCMs to achieve a high rate of carboxylation to oxygenation (e.g., Raven et al., 2011). The diatom Thalassiosira pseudonana uses extracellular carbonic anhydrase to take up HCO₃ directly (e.g., Nimer et al., 1997), the activity of which is down-regulated under elevated CO₂ levels (Burkhardt et al., 2001; Chen and Gao, 2003). In cyanobacteria, their CCMs can also be turned off at very high CO₂ levels (Kaplan et al., 1980; Raven, 1991; Matsuda et al., 2001). As summarized by Gao and Campbell (2014), the down-regulation of CCMs not only decreases CO₂ affinity, it alters the energy balance in the cell, leading to changes in cellular respiration. A shift in cellular pH may further increase the cellular energy allocation associated with the transport of ions across the cell membrane (e.g., Flynn et al., 2012). Both T. pseudonana and Phaeodactylum tricornutum showed enhanced rates of photorespiration, up to 23-27%, under conditions of elevated CO2 (Gao et al., 2012a; 2012b).

Diatoms are NO₃ opportunists. For example, in river-dominated

estuaries and upwelling systems, the occurrence of many rapidly growing diatom species has been highly correlated with the large and/ or frequent additions of NO3⁻ (e.g., Goldman, 1993; Lomas and Glibert, 1999). Diatoms are typically the dominant protist in NO₃-rich water columns during spring blooms. Marine pelagic ecosystems with predominantly NO3⁻ sources are often dominated by diatoms (e.g., Kudela and Dugdale, 2000; Wilkerson et al., 2000) and typically have short, efficient food webs at the base of major natural fisheries (e.g., coastal Peru) and high rates of export of organic matter from the photic zone (e.g. Eppley and Peterson, 1979). Diatoms are thus at a seeming disadvantage with a shift in N form away from oxidized N to more chemically reduced forms of N (Glibert et al., 2016). Nearly 60% of all N fertilizer now used worldwide is in the form of urea (CO(NH₂)₂; Constant and Sheldrick, 1992; Glibert et al., 2006, 2014a; IFA, 2014). Moreover, the uptake of NO3⁻ and its reduction to NH3 generally decreases at higher temperatures, especially above 15-18 °C (e.g., Lomas and Glibert, 1999 and references therein; Glibert et al., 2016), further suggesting that diatoms are negatively impacted as temperatures rise.

Numerous examples are emerging from direct experiments showing that qualitative changes in nutrients have effects on community composition even when the ambient nutrients are seemingly in the saturating portion of the response curve. In mesocosm studies, Glibert and Berg (2009) showed that NO_3^- uptake was directly related to the fraction of the community as diatoms, while the proportion of NH₄⁺ uptake was directly proportional to the fraction of the community as cyanobacteria. Similarly, in experiments conducted in the nutrient-rich San Francisco Bay Delta, proportionately more chlorophyll a and fucoxanthin (generally indicative of diatoms) were produced in enclosures enriched with NO3⁻ than in treatments with the same total N enrichment as NH_4^+ . In the latter case, proportionately more chlorophyll b (generally indicative of chlorophytes, i.e. green algae) and zeaxanthin (generally indicative of cyanobacteria) were produced (Glibert et al., 2014b). Toxic cyanobacterial species also appear to predominate over diatoms when N is supplied in chemically reduced relative to oxidized forms in the hypereutrophic Lakes Taihu, China, and Okeechobee, Florida (McCarthy et al., 2009), although these cyanobacteria can also grow when NO_3^- is the available form. Harris et al. (2016) reported that cyanobacterial biomass increased in Midwestern lakes when the proportion of NH4⁺ relative to NO3⁻ increased. In the eutrophic West Lake, Hangzhou, China, Jackson (2016) showed, using mesocosm experiments, that enriching the already-nutrient-rich waters with chemicallyreduced N substrates resulted in increasing amounts of cyanobacteria and chlorophytes. In similarly conducted experiments, enriching waters from a different eutrophic West Lake, this one in Florida, with NH4⁺ resulting in increased picocyanobacterial abundance, while NO₃ plus PO₄³⁻ enrichment resulted in diatom proliferation (Shangguan et al., 2017; Fig. 3a, b). There was also a loss of peridinin-containing dinoflagellates in the NO₃⁻ treatment and of cyptophytes in the NH₄⁺ treatment (Fig. 3a, b). Domingues et al. (2011) also showed that enrichment by NH4⁺ in a freshwater tidal estuary favored chlorophytes and cyanobacteria, whereas diatoms were favored under NO3⁻ enrichment. A recent study by Berg et al. (2017) tested whether diatoms grow faster under NO₃⁻ than NH₄⁺ or whether non-diatoms grow faster under NH4⁺ compared to NO3, based on switching cultures between media every few days of growth. Their findings yielded highly variable results, with interpretations of their results confounded by the fact that the species tested varied in size by orders of magnitude, and that internal nutrient pool sizes were not measured, nor were internal pools depleted before measuring growth rates on the new media. Larger cells have larger internal pools which are depleted at different rates compared to small cells.

A recent synthesis of 16 years of monitoring, combined with enrichment bioassays, in the Qu'Appelle River basin of southern Saskatchewan, Canada, illustrates the complex intersection of climate and nutrient pollution for these hardwater lakes (Swarbrick et al., 2019). These lakes now experience cooler and prolonged springs due to earlier ice melt, but they also experience warmer summers. Nutrient responses are complicated. They have experienced greater vernal suppression of spring diatom growth (Fig. 3c) and greater summer stimulation–as well as earlier onset–of summer non-N₂-fixing cyanobacterial communities by NH_4^+ enrichment, and these responses were more pronounced when P levels were low. Experiments by Donald et al. (2011, 2013) showed, for one of these hypereutrophic lakes, that NH_4^+ enrichment led to a proportionately greater increase in cyanobacteria.

7. Mixotroph dominance emerges

Fundamental physiological processes, such as enzyme activities, generally project that nutrients should be acquired more efficiently by autotrophs under warming conditions (e.g., Cross et al., 2015). Thus autotrophs should be favored as nutrients and temperatures increase. Yet, nutrient imbalances seem to prevail in aquatic ecosystems, from eutrophic to oligotrophic. Among the many 'strategies' for coping with a non-stoichiometrically balanced environment is the acquisition of nutrients in an alternative form (Glibert and Burkholder, 2011). An important advancement in the understanding of HABs and their nutrition over the past ~decade has been the evolving recognition of the importance of mixotrophy. 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). Although many authors have suggested that mixotrophy is operable and advantageous in nutrient-poor habitats as a mechanism to supplement nutrient supplies (e.g. Granéli et al., 1999; Stibor and Sommer, 2003; Stoecker et al., 2006), it has also been suggested that mixotrophs are prevalent in nutrient-rich environments (Burkholder et al., 2008) especially where nutrients may be imbalanced proportions (Jeong et al., 2010; Glibert and Burkholder, 2011; Flynn et al., 2013).

Mixotrophy fundamentally changes our understanding of planktonic food webs, enabling primary producers to acquire nutrients directly from ingestion of prey such as bacteria and algal competitors, and even from their predators. Mixotrophs thrive in conditions where

simultaneous acquisition of light and nutrients become challenging. With light from above, but major nutrient sources typically from below, mixotrophs have been said to perform the grand écart (dancer's splits), by combining two normally incompatible tasks-a difficult accomplishment at best (Selosse et al., 2017). Mixotrophy is not simply additive or substitutional with photosynthesis; rather it is synergistic (Mitra et al., 2014). Thus, through mixotrophy, there is provision of additional nutrients (N, P, Fe) from feeding to support primary production, together with a contribution of C to supplement photosynthesis under conditions of light limitation (including night). Moreover, the ecophysiology (nutritional quality) of the component organisms present in the ecosystem affects not only their own growth potential but also the activities of others: the cellular composition of algae, for instance, has consequences for grazers and their emergent properties, with potential for a positive feedback loop generating ungrazable primary producers (Mitra and Flynn, 2006; Glibert et al., 2010).

Mixotrophic dinoflagellates can ingest a wide variety of different prey items, including bacteria, other algae and protists, and fish tissue (Nygaard and Tobiesen, 1993; Lewitus et al., 1999; Stoecker, 1999; Burkholder et al., 2001, 2008; Stoecker et al., 2006, 2017; Seong et al., 2006). The cyanobacterium Synechococcus has been suggested to be a food source for many mixotrophs (e.g., Jeong et al., 2005), due to its ubiquitous nature in both offshore and coastal waters, its potential for high growth rates (Kana and Glibert, 1987), its high N content relative to P (Finkel et al., 2010) and its co-occurence with many dinoflagellates (Murrell and Lores, 2004). The Florida red tide dinoflagellate, Karenia brevis, has the ability to graze Synechococcus at substantial rates (0.96–83.8 prey cells K. $brevis^{-1}h^{-1}$; Jeong et al., 2005; Glibert et al., 2009b), and to increase its growth rate upon feeding (Glibert et al., 2009b). Numerous examples of other species, such as Karlodinium veneficum (Adolf et al., 2008) and Margalefidinium (Cochlodinium) polykrikoides (Jeong et al., 2004; Gómez et al., 2017) have also been shown to obtain a growth rate benefit from mixotrophy (see review by Burkholder et al., 2008).

Essential elements such as N, P and C are typically rich in microbial prey and thus mixotrophy can provide a supplemental supply when there is an elemental imbalance in dissolved (water-column) nutrient substrates (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 that of their prey (e.g., Lundgren et al., 2016; Lin et al., 2017). 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., 2009b).

Most harmful dinoflagellates, haptophytes and raphidophytes are mixotrophs to some degree, many of which feed on their autotrophic competitors, and many of which themselves become prey for other mixotrophs (e.g., Park et al., 2006; Jeong et al., 2010). In some instances, toxins are used in the capture of 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; Glibert et al., 2016). Production of toxins rich in N might be regarded as a dissipatory mechanism, whereby cells acquire the nutrient(s) they need but release nutrients that are not needed (Glibert and Burkholder, 2011; Glibert et al., 2016). There are numerous examples from the marine literature that show that many HABs are indeed more toxic under conditions of elevated N:P ratios, i.e., under high N. As examples, under conditions of elevated N:P, haemolytic activity per cell increases by up to an order of magnitude in the prymnesiophytes Prymensium parvum and Chrysochromulina (now Prymnesium) polylepis (Johansson and Granéli, 1999), and neurotoxin production increases in the diatom Pseudo-nitzschia

multiseries and in the dinoflagellates *Karlodinium veneficum*, *Alexandrium* sp., and *Karenia brevis* (Granéli and Flynn, 2006; Hardison et al., 2013). Excess N and high N:P ratios have also been related to microcystin (MC) production under controlled culture conditions (e.g., Lee et al., 2000; Oh et al., 2000; Vézie et al., 2002; Downing et al., 2005; Van de Waal et al., 2009). Some *in situ* evidence, albeit weak, also suggests that increased N availability may influence the MC congener type to more toxic variants that have higher N content (e.g., Van de Waal et al., 2009) and that P limitation causes an increase in N-rich toxins of numerous HABs (Van de Waal et al., 2014). Toxin production and mixotrophy are, furthermore, synergistic: release of toxins may harm prey, releasing dissolved nutrients or make prey easier to capture that, in turn, can enhance growth rates.

Modeling of mixotrophy is advancing. Inclusion of mixotrophs within a simple nitrogen-phytoplankton-zooplankton-bacteria-detritus (NPZBD) model results in a substantial difference in planktonic trophic dynamics (Mitra et al., 2014). This is because food web dynamics are not merely a summation of a series of rate processes (and kinetic curves); they are an outcome of both the quantity and *quality* of the substrate (or food) provided. Global models including mixotrophy project production of larger cells that may sink faster, accelerating the biological pump (Mitra et al., 2014; Ward and Follows, 2016). While warming may predict an increase in smaller cells, and mixotrophy models may predict an increase in larger cells, these predictions may not be mutually exclusive. As noted above, small cells such as *Synechococcus* may serve as prey for mixtrophs and as food increases, so too may mixotrophic communities. Such changes are, however, dependent on nutrient conditions.

Recent modeling, based on experimental data on the mixotroph Karlodinium veneficum and its prey, Rhodomonas, grown individually under varying temperature, autotrophic conditions, and in mixed batch cultures in which N:P stoichiometry (molar N:P of 4, 16 and 32) of both predator and prey varied, illustrate these complex dynamics. Results showed that biomass of K. veneficum was highest when it was parameterized as a mixotroph and when it consumed prey under the highest N:P conditions considered (Lin et al., 2018a,b). The modeled scenarios under all N:P conditions showed large differences between mixotrophic and autotrophic growth, but these differences varied with temperature. When inorganic nutrients were in balanced proportions, lower biomass of the mixotroph was attained at all temperatures in the simulations, suggesting that natural systems might be more resilient against Karlodinium HAB development in warming temperatures if nutrients were available in balanced proportions. The complexities shown in this model with regard to the differential impacts of temperature on the growth of mixotroph predator and prey, parallel those expected under (de)eutrophication scenarios with ocean acidification (Flynn et al., 2015). Fully understanding-and thus predicting-changes in the competitive advantage of mixotrophic species under multi-stressor environments (light, temperature, pH, nutrients) will require a concerted effort in physiology-modeling research in order to aid ecosystem management.

8. Conclusions

The conclusions of this paper mirror those of other recent reviews on HABs, eutrophication and climate that focus on the complex nature of this nexus (e.g., Fu et al., 2012; O'Neil et al., 2012; Boyd and Hutchins, 2012; Gobler et al., 2016; Glibert and Burford, 2017; Glibert and Burkholder, 2018). There is much we still do not know regarding physiological ecology across function groups, how to correctly parameterize rates, characterize traits, and how they are externally driven and internally dynamically regulated. It should be clear, however, that while some HABs follow simple nutrient supply responses, simplistic pressure-state responses are insufficient to understand when and why specific HABs respond to nutrients and how these responses change with other environmental conditions. That nutrition plays an important role in the expansion of HABs should be obvious with our contemporary understanding of phytoplankton physiology and ecological stoichiometry. That changing climate also reinforces the expansion of HABs should also be intuitive. Understanding that changes in growth rate are not the only metric by which success of one taxa (i.e., a harmful species) should be measured is less intuitive; those of the whole community-from competitors to consumers-must be considered. Furthermore, simplistic approaches to curb HAB growth by continuing to reduce the "limiting" nutrient fails to advance us from a dose-response mindset; as emphasized here, stoichiometry changes do matter for biodiversity (Glibert, 2017). Understanding the full suite of processes and factors that underlie variable stoichiometry at all scales-and for elements bevond 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 a global ocean should motivate both new model architectures and new experimental investigations that support them.

While the challenges of controlling nutrients and managing HABs will continue to be great, there are also many opportunities to continue to advance the understanding of HABs and environmental changes. Effects on cell size are projected to be great, but conflicting. Grazing effects, allelopathy, biogeochemical fluxes are also part of the environmental suite of factors regulating their growth and there is much we have yet to know regarding how these interactions change with stoichiometric changes or climate related factors. The plasticity of nutritional pathways, as well as the plasticity of food web interactions, including mixotrophy, creates immense challenges for model constructs. Lastly, while the steps that have been taken to reduce P usage should be praised and encouraged, and concern remains about the comparatively limited options for reducing global CO₂, we increase the likelihood of more blooms, more toxins, and more ecosystem impacts in more places if our escalating N footprint is also not addressed.

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