Future HAB science: Directions and challenges in a changing climate

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ABSTRACT

There is increasing concern that accelerating environmental change attributed to human-induced warming of the planet may substantially alter the patterns, distribution and intensity of Harmful Algal Blooms (HABs). Changes in temperature, ocean acidification, precipitation, nutrient stress or availability, and the physical structure of the water column all influence the productivity, composition, and global range of phytoplankton assemblages, but large uncertainty remains about how integration of these climate drivers might shape future HABs. Presented here are the collective deliberations from a symposium on HABs and climate change where the research challenges to understanding potential linkages between HABs and climate were considered, along with new research directions to better define these linkages. In addition to the likely effects of physical (temperature, salinity, stratification, light, changing storm intensity), chemical (nutrients, ocean acidification), and biological (grazer) drivers on microalgae (senso lato), symposium participants explored more broadly the subjects of cyanobacterial HABs, benthic HABs, HAB effects on fisheries, HAB modelling challenges, and the contributions that molecular approaches can bring to HAB studies. There was consensus that alongside traditional research, HAB scientists must set new courses of research and practices to deliver the conceptual and quantitative advances required to forecast future HAB trends. These different practices encompass laboratory and field studies, long-term observational programs, retrospectives, as well as the study of socioeconomic drivers and linkages with aquaculture and fisheries. In anticipation of growing HAB problems, research on potential mitigation strategies should be a priority. It is recommended that a substantial portion of HAB research among laboratories be

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directed collectively at a small sub-set of HAB species and questions in order to fast-track advances in our understanding. Climate-driven changes in coastal oceanographic and ecological systems are becoming substantial, in some cases exacerbated by localized human activities. That, combined with the slow pace of decreasing global carbon emissions, signals the urgency for HAB scientists to accelerate efforts across disciplines to provide society with the necessary insights regarding future HAB trends.

1. Introduction

There is emerging evidence that climate change already may be impacting the frequency and severity of harmful algal blooms (HABs) in marine, brackish, and freshwater environments (Berdalet et al., 2016; Gobler et al., 2017; McCabe et al., 2016; Paerl, 2016). The underlying premise is that climate drivers are altering environmental conditions in ways that may lead to: 1) HAB species becoming more competitive relative to non-HAB species within plankton assemblages, 2) enhanced toxin production by toxic HAB species, and 3) an increased likelihood and severity of high biomass HABs developing due to changes in hydrology. Nevertheless, the current projections of how climate drivers may influence the prevalence of HABs remain largely speculative (Wells et al., 2015), although there are indicators that increasing storm and tropical cyclone severity may be promoting some HABs (e.g., Paerl et al., 2018). Some fundamental responses are plainly anticipated; for example, projected increases in surface water stratification in principle favor an increased presence of cyanobacteria and dinoflagellates (e.g., Gobler et al., 2017), and increased precipitation is recognized as a driver of phytoplankton ecology (Thompson et al., 2015). These responses, however, will not be universal, with many other factors influencing the outcome of HAB dynamics every year in each location. It also is reasonable to anticipate that unexpected linkages will emerge (e.g., McGillicuddy et al., 2011), that there will be non-linear responses both leading to and diminishing the responses of HAB populations, and that there may be ecological phase shifts (Bathiany et al., 2018). As Stephen Carpenter recently stated: We cannot rely on the past to solve the future (Redfield Lifetime Achievement Award lecture, ASLO Annual Meeting, 2019). However, the basic principles of algal growth and competition, and building blocks of the HAB cells and HAB-enabling environments, are being directly and indirectly altered by changes in the physical state (climate) and the social state (anthropogenic activities) of the Earth. With these foundational limits, the best approximation of the future can be discussed, projections established, and conclusions ascertained.

A Scientific Symposium on Harmful Algae and Global Climate Change was held in May 2015 at the University of Gothenburg (pices.int/meetings/international symposia), where 59 scientists from 23 nations gathered to consider the future directions for HAB and climate change research. The objectives of the Symposium were to bring together plankton physiologists, ecologists, oceanographers, modelers and climate change specialists to develop a consensus on the priority research directions for future HAB and climate change funding, develop "proactive" research strategies build from rigorous, testable hypotheses to guide scientists, managers and the public on what environmental and HAB changes are projected, and consider realistic designs for observing infrastructures (combining research studies, detection schemes, observing systems) to capture the critical datasets needed to assess HAB patterns in relation to measurable indicators of climate change. This Symposium was designed to enable a larger community assessment of the outcomes published from an earlier, small workshop addressing a subset of issues relating climate change to HABs—temperature, precipitation, salinity, stratification, light, ocean acidification, nutrients, and grazing—(Wells et al., 2015), and to broaden the topics considered to include cyanobacterial HABs, benthic HABs, HAB effects on fisheries, HAB modeling challenges, and the potential contributions of molecular approaches to shed light on changes in HABs.

We present here a summary of these breakout group discussions as a starting point for considering new coordinated strategies for studying HAB phenomena. Each breakout group was delegated to refine a short list of what participants felt were the most urgent questions, a list of critical research topics, and to identify the needs for new tools, experimental designs, observation infrastructures and linkages to other existing research programs. The increasingly rapid advance of climate change drivers in oceanographic and ecological systems raises the urgency with which HAB researchers need to extend their research across disciplines, to maximize extant opportunities, and develop new coordinated efforts. The intention here is to provide a basis for moving towards this goal.

2. What is a harmful algal bloom?

Although seemingly uncomplicated, defining a "harmful algal bloom" is a deceptively complex undertaking. The designation "harmful algal bloom" initially was conceived decades ago to describe toxic events that could impact humans, but it has evolved over more recent decades to include events causing "negative" ecological impacts. The recent passing of Prof. Ted Smayda (Thomas, 2017), who contributed much to this Symposium, reminds us of his seminal commentary on the difficulty of defining and studying harmful algal blooms (Smayda, 1997). As a societal term, the scientific definition is inexact, but the term has contextual understanding. Sometimes the event is "harmful," sometimes the event is simply esthetically annoying; sometimes the biomass is easily observed and the term "bloom" refers to an elevated presence, usually involving out competing other species, yet sometime the HAB species is a relatively minor intrusion of an undesirable species into the common community. For example, action levels for Paralytic Shellfish Poisoning (PSP) closures of bivalve fisheries are as low as 100 cells L^{-1} of *Alexandrium* in the Gulf of Maine (Maine Department of Marine Resources) and 40 cells L^{-1} in Scotland (https://www.foodstandards.gov.scot/business-and-industry/industry-specific-advice/fish-and-shellfish). Such "minor presence" HABs raise additional difficulties to their study given that factors regulating a low-level presence may well have much finer thresholds than those determining which species dominate in more traditional phytoplankton "blooms". Moreover, the discussion here is limited to extant forms of HABs—those events and species that had been classified as such by society—but how confident are we that we have identified all of the problematic species, conditions, or even syndromes that affect human and ecosystem health? Are there "cryptic" harmful species that so far have not reached the "presence" levels, or appeared at the sensitive times, to be recognized as "harmful"? If so, will climate drivers lead them to become better established in some regions of the future oceans? Is the unexpected outbreak of a new genotype of toxic *Alexandrium catenella* along the east coast of Tasmania an example of this risk (Trainer et al., 2019), along with new manifestations of high-biomass, non-toxic green *Noctiluca* blooms in the Arabian Sea and Gulf of Oman (Harrison et al., 2011)? Although the risk of these "black swan" emergences (Taleb, 2007) cannot be judged *a priori*, the increasingly rapid rates of environmental change highlight the need for vigilance in appraising how we define "harmful blooms".

Despite these complications, the need to formally define "HABs" is not esoteric—it's critical. Testing hypotheses linking climate change to increasing HABs demands quantifiable and *globally uniform* metrics for the presence and intensity of HABs to compare against exacting measures of regional environmental change. These threshold metrics for

HAB events will differ among HAB syndromes (at a minimum) and these necessary definitions should be distilled from research community deliberations, perhaps best conducted (and periodically reviewed) in special sessions organized by GlobalHAB (http://www.globalhab.info) in conjunction with biannual meetings of the International Society for the Study of Harmful Algae (ISSHA, https://issha.org).

3. The physiological effects of temperature

Each organism has a unique physiological temperature range that delineates the potential window of opportunity for their growth success; HAB species are no different in this regard. Individual species differ in optimal temperatures for cell division rates, photosynthesis, and, likely also for feeding, as many HAB species are mixotrophs. Yet, climate induced temperature changes are multi-faceted and scalar: cellular optimal temperature, thermal mixing, catchment biogeochemistry and DOC release, seasonal and autumnal mixing, desynchronization of grazing activity from phytoplankton growth. As such, the temperature effect on HAB success (Stawiarski et al., 2016), and phytoplankton in general, is difficult to isolate due to the multitude of overlapping or sequential changes in the physical structure of the water column, nutrient supply and seasonality, and light availability (Behrenfeld et al., 2006; Eppley, 1972; Johnson et al., 2006). Largely for this reason, while increasing *in-situ* temperature has an apparent positive correlation with some HABs (e.g., Gobler et al., 2017; Paerl and Huisman, 2008), there are few experimental data that can show direct mechanistic linkages between increasing temperature and improved HAB species physiology and competitive advantages over non-HAB species in the same assemblages (Lewitus et al., 2012; Wells et al., 2015). Temperature also may have indirect effects on the physiology of HAB species through affecting the optimal prey species of mixotrophic HAB species (e.g, Lin et al., 2018). Changes in temperature maxima, or the rate of seasonal temperature change, may alter the magnitude and timing of excystment of overwintering HAB stages (Fischer et al., 2018), though the role of temperature in cyst and resting state germination is not well defined for most HAB species (and typically absent from models; Flynn and McGillicuddy, 2018). More broadly, even small changes in HAB phenology and spring transitions of surface waters may increase or decrease the potential biomass of HAB species (e.g., McGillicuddy et al., 2011). Temperature related changes in cellular growth rates also can affect cellular toxin concentrations (e.g., Thorel et al., 2014; Trainer et al., in press; Toseland et al., 2013), meaning that future HAB impacts need to be considered in terms of both HAB growth and the cellular rates of toxin production (e.g., Basti et al., 2015).

There are several key questions that define our limited knowledge of how temperature will influence HABs. First and foremost, the intuitive presumption among many HAB scientists is that warming will increase the likelihood of HAB prevalence and intensity in the future oceans, but, excluding a limited number of exceptions (e.g., Gobler et al., 2017; McLeod et al., 2012), there are few studies to quantitatively determine if temperature alone is a significant driver of HAB events. Gobler et al. (2017) linked regional scale increases in surface water temperatures to model an increasing prevalence of HAB species, an essential first step, but is it possible to identify range expansions, or contractions, that have coincided with warming temperatures? Indeed continental warming patterns have matched the northward trends in some freshwater cyanobacterial HABs (Paerl, 2016), but the evidence in marine systems is far less distinct. For example, despite warming in waters of the United Kingdom the predicted increase in *Dinophysis acuminata* since 1982 in the model of Gobler et al. (2017) was not evident in the Continuous Plankton Recorder (CPR) record from the region (Dees et al., 2017). The current magnitude of warming may still be too small to elicit notable and recurrent effects on HABs, or other factors (e.g., prey availability to heterotrophic *Dinophysis*, predation or other ecological interactions) are limiting temperature-driven increases in these HABs. Massive blooms of *Noctiluca scintillans*, a species that favors well stratified conditions, have

become established in the Arabian Sea over the last decade which may be related to climate change (Lotliker et al., 2018), although there is argument that it instead I driven by the combination of anthropogenic nutrient inputs and low oxygen rather than climate (Gomes et al., 2014). However, McLeod et al. (2012) has documented climate-driven range expansion of *N. scintillans* into the Southern Ocean, likely via warm-core eddies, a complicated mechanism by which temperature allows for range expansion without the final ecosystem undergoing temperature changes.

By accepting that the best initial predictor of temperature-induced changes is the ability of the HAB species to thrive or survive at elevated temperatures, ecophysiological studies can provide an initial understanding of direct temperature effects on HAB competitiveness. But how should this be done? There can be differences in temperature optimal among species or strains in both in culture (Boyd et al., 2013; Thomas et al., 2016) and nature (e.g., Chen et al., 2015, also summarized in Wells et al., 2015)—to what extent will strain variability affect our projections of temperature-driven effects on HAB species competitiveness? Common garden style studies using multiple strains across geographic regions would greatly accelerate our understanding of these and other issues. Alternatively, one or two strains of each problem HAB organism should be identified as "reference" clones for comparison with local strains from other regions. Use of more recently isolated strains in experiments would help to ensure that physiological traits have not become profoundly altered by extended exposure to standard algal culture regimes, although it is not clear how important this problem may be for most HAB species. It remains crucial to include regionally co-occurring non-HAB species with HAB species in these studies to provide the insights on competitive outcomes essential for model development.

Beyond cellular-based responses, the changes in seasonal temperature patterns may influence HABs simply by generating longer windows of opportunity where conditions are more physiologically amenable for HAB development (e.g., Moore et al., 2011; Paerl and Otten, 2013). Similar transitions in associated parameters (e.g., light, nutrients, prey for mixotrophs, etc.) may introduce multiplicative interactive effects with temperature that should be considered when studying the physiological response of HAB species to temperature increase.

With temperatures of coastal waters generally increasing over the past few decades (e.g., Pachauri and Meyer, 2014), do quantitative indicators of temperature/HAB occurrences already exist? Mining available public health monitoring data among the wide diversity of coastal and oceanographic regimes is a logical starting point and this effort now is underway (Hallegraeff et al., in prep.). HAB time series that are collected for regulatory purposes would increase in value if there was funding for parallel collection of environmental information. Comparative field studies from HAB-prone regions where oceanographic data are available will be essential but will depend upon more open sharing of HAB data among countries, and foresight from funding agencies to support these longer-term projects.

In summary, the apparent correlation between increasing temperature and increasing occurrence of some HABs, particularly notable for freshwater cyanobacteria but much less consistent for marine HABs, does not demonstrate causation, but reflects on the importance of temperature in the biological and physical structure of the environment where HABs emerge. While many HAB species grow faster at higher temperatures in laboratory studies, the same is true for other plankton. The hypothesis that increasing temperature mechanistically drives increasing HABs needs critical assessment at three levels.

1) Experimental studies should be designed to test whether HAB species have a demonstrated physiological advantage at higher temperatures over at least some regionally, or locally, abundant non-HAB species. These studies need to account for regionally relevant growth conditions during HAB development—e.g., representative nutrient inputs and light conditions rather than standard

"cookbook" culturing norms—to best inform model development.

2) There is a clear trend of increasing surface water temperatures in freshwater and marine systems over the past few decades, so long-term datasets within globally distributed HAB monitoring programs offer a chance to statistically test the HAB/temperature relationship, as well as the temperature/HAB relationship (i.e., is increasing temperature more often than not associated with increasing HABs). These studies should be restricted to those regions not suffering simultaneous increasing impacts from anthropogenic runoff. Although these observational data alone cannot inform on the underlying linkages, when combined with mechanistic-based laboratory studies these data would provide a more solid basis for testing the HAB/temperature hypothesis. The northward trend in increasing freshwater HABs provides a good platform for investigating temperature thresholds and forecasts for future HAB development in lakes and rivers, again independent of increasing anthropogenic nutrient loading.

3) Given that most HAB monitoring datasets either lack or have only limited records of oceanographic data, new HAB observational programs will be essential for testing the hypothesis that increasing temperature drives HAB development. Ideally, these observatories would best link with existing observational sites where possible, where the core measurements of phytoplankton species composition and abundance over biologically relevant time frames, their toxicity, surface water temperatures as well as other oceanographic parameters (e.g., nutrients, winds, light, etc.) can be collected. The progressive implementation of the GOOS, with HABs included as an Essential Oceanographic Variable (GOOS_BioEco, 2018), illustrates progress in this direction. Given that the extent of ocean warming is greatest in high latitude waters, particularly in the Arctic, there should be a priority placed on measuring the presence/absence and success of HAB species within high latitude freshwater and marine plankton communities. These may serve as the most sensitive indicators —the "canaries in the mine"—of climate/HAB changes (Hobday et al., 2016).

4. Effects of increasing stratification

A widely-held paradigm is that many HABs are associated with stratification, but we recognize that most well-stratified waters do not harbor HABs. Vertical stratification and mixing (turbulence) of the water column strongly affects phytoplankton dynamics in all aquatic ecosystems, and can modulate HAB dynamics in combination with other physical processes (GEOHAB, 2013; Timmerman et al., 2014). While surface warming increases stratification, there is no reason to expect that all future coastal environments will become more stratified (Bopp et al., 2013). Increased global temperatures will favour stratification in many locations, and it will be enhanced by greater precipitation and runoff in others. Even so, higher temperatures also will lead to more intense storms and tropical cyclones (US Climate Change Report 2018) that, when combined with tidal mixing forces, increasing sea level and other factors, suggest that temporal and spatial patterns of stratification will differ and become more variable in the future (Table 1).

HAB responses to changes in stratification will depend upon local geography such as catchment characteristics and river, estuarine, bay, and coastal geomorphology. In addition, future projections of more intense precipitation events (e.g., Pachauri and Meyer, 2014) will influence the timing and magnitude of river flow, adding further complexity to projections for specific regions.

In spite of the complications and the range of possible mechanisms, any increase in stratification is expected to exacerbate the potential for HABs in shelf and marginal seas. Many dinoflagellate, raphidophyte, and cyanobacterial HAB species have physiological ranges and life history traits that make them strong competitors under stratified conditions (Smayda and Reynolds, 2001). For example, many HAB species

are strong vertical migrators which enables them to access nutrients across shallow pycnoclines (Kudela et al., 2010). Some are well adapted to assimilate recycled forms of nutrients and many are strongly mixotrophic when nutrients are low, a frequent occurrence in stratified water bodies. Others can proliferate in contiguous hidden thin layers in coastal regions (Rines et al., 2002; Timmerman et al., 2014). Many if not most HAB flagellate species are photo-phagomixotrophic, with potential for profound impacts on trophic dynamics under low nutrient conditions (Flynn et al., 2018).

Both the timing and the magnitude of changes in stratification will be important in determining HAB responses (Fig. 1). In temperate to higher latitudes, the timing of the seasonal onset of stratification is important for the development of diatom spring blooms (Doney, 2006). With increased warming, and potentially earlier peak runoff, more rapid onset of stratification leads to earlier spring blooms, more protracted periods of stronger stratification over the summer months, and the opportunity for HAB species to be present for a greater portion of the year (Moore et al., 2011). However, the trend towards stronger warming, and perhaps runoff, during spring also can intensify spring diatom blooms, in some cases leading to lower nutrient retention in subsequent summer stratified surface waters and thereby reducing the potential for dinoflagellate and other flagellate HABs to develop. The noticeable absence of *Alexandrium* HAB events during 2010 in the Gulf of Maine has been attributed to this mechanism (McGillicuddy et al., 2011). Moreover, in regions where global warming leads to stronger stratification year-round, nutrient recharge of the surface mixed layer during winter will be more restricted, leading to smaller subsequent spring blooms. Indeed, existing observations of long-term trends in temperature suggest that some regions are newly experiencing greater stratification in winter (e.g. Seto Inland Sea; Tasman Sea).

Other oceanographic features such as frontal regions are also likely to be impacted by climate change. Frontal regions are sites of elevated phytoplankton biomass (Franks, 1992) and these features can be locally or regionally important in the formation of HABs, or act as barriers to their advection (Hickey et al., 2013; Paterson et al., 2017). Changes in freshwater inputs to coastal regions could alter the role of rivers as either conduits or barriers of HAB transport to beaches (Hickey et al., 2013). Similarly, climate change is likely to influence the upwelling of cool, nutrient-rich deep water that can promote HAB events, such as what is observed to occur in the important shellfish production region of Galicia (Spain) (Diaz et al., 2016).

Testing the hypothesis that intensified stratification is linked to increasing HABs in the future ocean will be difficult because there is very little understanding of what drivers lead to present day HABs in well stratified systems. Nevertheless, there are three ways to better assess this relationship.

1) Through retrospective studies of HAB occurrences against concurrent measures (or estimates) of stratification intensity (i.e., density differences across the pyncnocline). Most HAB monitoring programs focus only on human health and do not include the needed oceanographic or limnological measurements, but it should be possible in some cases to link HAB data with those from local observatories to begin this assessment.

Table 1
Possible future scenarios for stratification.

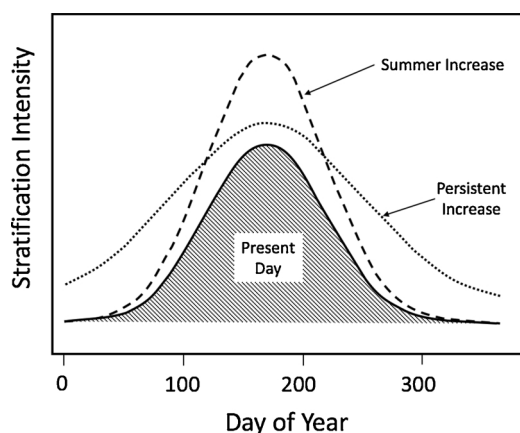| Driver	Expected stratification response
Increasing temperatures	Increase
Increased precipitation	Increase or decrease, location dependent
Changing wind speeds	Decreased and enhanced
Increased evaporation	May decrease
Sea level change effects on tidal and coastal currents	May increase or decrease

Fig. 1. Generalized possible future stratification scenarios. HABs may be expected to be more prevalent under either future scenario in at least some regions.

2) Global climate models have progressed to where there is emerging consensus on broad regional differences in the rate future temperature change. Downscaling (higher resolution) physical models should be developed to refine these insights to highlight localized regions that may experience more rapid regional surface waters temperature changes or increased interannual variability. Although stratification intensity cannot be estimated from surface water temperatures alone, these climate "hot spot" forecasts would help focus regional observational resources to test the hypothesis that stratification enhances HABs (Hobday et al., 2016).

3) Measures of increased stratification intensity must be integrated with physical, chemical and biological data from long-term coastal or lake observatories, ideally by augmenting these observatories with phytoplankton community and HAB species abundance measurements. Simply linking HABs to increased stratification does not provide a mechanistic explanation for the effect; i.e., the detailed understanding needed to determine how well the findings can be extrapolated to other stratified systems. Knowledge gained on HABs in stratified systems obtained over the last 20 years of collaborative international research provides a good foundation for obtaining more detailed understanding of how future scenarios for stratification could influence HABs (Berdalet et al., 2014).

5. Effects of ocean acidification

Increasing atmospheric pCO_2 over the past few decades has generated measurable decreases in the pH of surface waters in offshore, coastal and upwelling marine regions, as well as in freshwater environments (Doney et al., 2009; Feely et al., 2008; Paerl and Paul, 2012). To what extent do these changes in pH affect the physiology of phytoplankton in general, and HAB species in particular? While there are a rapidly growing number of studies considering the effects of increasing dissolved CO_2 on phytoplankton and HAB species (e.g., Dutkiewicz et al., 2015; Flynn et al., 2015), little consensus is found in the literature. For example, decreases in pH shift the carbonate system to decrease bicarbonate concentrations and increase dissolved pCO_2, thereby increasing carbon availability for photosynthesis (Beardall et al., 2009; Raven and Beardall, 2014). This process downgrades the value of metabolically costly carbon-concentrating-mechanisms (CCMs) that many species of phytoplankton have evolved; a change that may alter the competitive balance among species (Beardall et al., 2009). Some HAB species lack CCMs while others have less effective CCMs than other phytoplankton (Kremp et al., 2012; Rost et al., 2003), so decreasing pH has the potential to influence competitive interactions among HAB and non-HAB species. This mechanistic-based scenario, however, has not yet been demonstrated to occur. Moreover, if it does,

what degree of pH change is needed to affect HAB species growth rates or biomass yields? Even small improvements in growth rates, or competitive success, can make HABs significantly more problematic (e.g., Dutkiewicz et al., 2015; Flynn et al., 2015), particularly as a comparatively small number of some toxic species can generate HAB conditions within larger, non-toxic algal assemblages. On the reverse side, high biomass blooms lead to basification, or increased pH, due to rapid cellular uptake of CO_2. So while efficient carbon concentrating mechanisms may have little importance during early bloom stages under ocean acidification conditions, their value would be magnified as phytoplankton biomass increases, potentially impacting successional patterns (Flynn et al., 2015). This type of conceptual exercise lends itself well to modeling how these scenarios influence the magnitude of relative change in the growth rates of HAB/non-HAB species.

Decreasing seawater pH also influences other cellular processes, including maintaining membrane potential, enzyme activity, and energy partitioning (Beardall and Raven, 2004; Giordano et al., 2005). For example, proton gradients across cell membranes regulate a number of critical cellular uptake processes (e.g., Giordano et al., 2005). What level of pH change is needed to influence the macronutrient uptake capacity by phytoplankton, and does this differ among HAB and non-HAB species? There is evidence that trace metal availability also may change with pH, decreasing in some places and increasing in others (Breitbarth et al., 2010; Gledhill et al., 2015b; Shi et al., 2010). To what degree may these changes affect cell physiology and toxicity? For example, any pH-driven decrease in iron availability can increase the production of domoic acid in *Pseudo-nitzschia* species (Maldonado et al., 2002; Wells et al., 2005)—are the same trends found for other HAB species and if so under what pH conditions? To what extent are other metabolic processes affected by changes in the efficiency of proton pumping across the cellular membrane? It also is important to note that pH at the organism interface (i.e., next to the plasma membrane) is altered through their activities over the course of the day, and differs from bulk water conditions (Flynn et al., 2012).

As noted, one of the competitive features of many toxic and fish-killing HAB species is their ability to actively migrate vertically by swimming, but lowered pCO_2 can affect the swimming ability of at least one HAB species – the raphidophyte *Heterosigma akashiwo* changes its swimming behavior at lower pH in ways that may impede the formation of harmful surface blooms (Kim et al., 2013). Will the swimming behaviors of other HAB species be affected by lower pH in ways that may alter their nutrient acquisition potential or mixotrophic activities? Impacts of OA upon grazers is also an important, and often underestimated, aspect of plankton dynamics (Cripps et al., 2016, 2014). If copepod growth and activity are adversely affected then the succession and success of non-HAB and HAB species also will be affected, irrespective of whether there is a direct primary link from OA to HAB growth.

One of the problems often overlooked by marine scientists is the extraordinary difficulty in obtaining precise and accurate measurements of pH in seawater. Simple use of laboratory glass electrodes with National Bureau of Standards (NBS), or equivalent (e.g., red, yellow, blue) pH standards gives substantially inconsistent and inaccurate values that cannot be quantitatively compared with ocean observing systems. Frequent calibrations with certified seawater standards are essential, and temperature control is needed (Dickson et al., 2007). Due to these problems, marine chemists use less problematic measurements of alkalinity and dissolved inorganic carbon to calculate pH, thereby attaining far greater precision and accuracy. Although high levels of precision and accuracy in pH (~ ± 0.005 pH) are needed for quantifying relevant changes in the seawater carbonate system, pH measurement protocols are equally demanding at the lower levels of precision likely needed for understanding biological impacts. Attaining some consensus among HAB scientists on methodologies, precision, and accuracy of pH determinations *for biological studies* is necessary before the findings among studies can be quantitatively interpreted (e.g., McLaughlin et al.,

2017).

Much of the research that has been done studying acidification effects on HAB species has been empirical. While informative, it will be essential to understand the mechanistic basis for these responses to extrapolate the findings to other species or regions. That is, as a field, HAB research should emphasize more the conceptual mechanisms and hypothesis testing of the underlying reasons why pH might alter functional responses (e.g., Hansen et al., 2007). Using a mechanistic approach, is it possible to identify trait–based functional types of HABs that respond in uniform ways to changes in pH? As always, the danger of focusing on a single stressor may lead to false insights (Boyd et al., 2018); how do the functional responses to pH vary under realistic multi-stressor conditions? For example, interactions between pH and nutrient stress are complex, especially when compared among species (Flynn et al., 2015). Control of test conditions is not possible in (natural multistressor) field (*in-situ*) studies, so it will be important to measure as wide a variety of environmental parameters as possible (e.g., temperature, light, macronutrients, micronutrients, community composition, etc.) in appropriately controlled laboratory settings if the findings are to be adequately interpreted and extrapolated to other regions.

Field observations linking surface (or subsurface) ocean pH to HABs, such as incorporating measurements of HAB species abundance with the Global Ocean Acidification Observation Network (GOA-ON; goa-on.org), will be invaluable for quantifying the relationships between HABs and ocean acidification, but determining the underlying causes for trends will depend upon experiments under well-controlled laboratory systems. The hypothesis that ocean acidification enhances the competitive ability of HAB species can be readily addressed within our current experimental capabilities. Mechanistically, the studies can be separated, based on our current knowledge, into hypothesis-testing of pH effects on carbon acquisition, the uptake of macro- and micro-nutrients, and the effect on the motility of HAB species (i.e., potential for vertical migration and mixotrophy); all amenable for study under well-controlled laboratory conditions. It bears emphasis that these studies should include regionally co-occurring non-HAB species so that competitive outcomes can be evaluated. The hypothesis that cellular toxin production and cellular toxin concentrations are enhanced at lower pH needs to be addressed across all toxic HAB syndromes to guide modelers on parameterizing cell abundance/toxin impact in their simulations. Last, but critically important, all of these laboratory studies need to adhere to the recommendations for pH measurement in seawater (Dickson et al., 2007; Riebesell et al., 2010) to enable their extrapolation to natural waters.

6. HABs and nutrients

Climate change will directly influence nutrient supply and composition to/in coastal waters as a consequence of altered precipitation and hydrological intensification, modified biogeochemical remineralization and weathering in catchments, and stronger or weaker vertical mixing from wind forcing and storms. The current projections indicate increased precipitation in some regions (e.g., southeast Asia, tropical East Africa), while decreases are likely in others (e.g., southern Europe, southwestern USA) (Pachauri and Meyer, 2014). Regional shifts in absolute precipitation or hydrological intensification (extreme events ranging from intense rainfall events to extended droughts) are expected to have long-term (seasonal-to-decadal scale) effects on salinity, stratification and turbulence as well as the vertical structure of water columns. While changes in terrestrial runoff likely will dominate climate-driven deviations in nutrient flux to coastal waters, wind forcing and storms (i.e., vertical stability of the water column) also will influence the entrainment, availability and vertical flux of nutrients in the pelagic and benthic environments. It probably will be the combination of climate-driven hydrologic forcing at the local level (wind mixing, flushing of coastal bays, changes in estuarine stratification), as well as large-scale changes (e.g., ocean currents and upwelling) that need to be

considered in order to justify these factors as climate drivers of HABs initiation or stability. The central questions then are to what extent do climate drivers affect the primary drivers of species selection and dominance: supply rates, composition, and availability of nutrients; the consequences of these changes on nutrient quality (speciation, ratios, etc.); and whether these, in turn, alter the competitive success of HAB species over non-HAB species.

Nutrients as a driver should be defined in a broad sense. While climate effects on the availabilities of macro-nutrients (N, P, Si) are important, so too are the effects on micro-nutrients (trace metals, vitamins) and 'prey' (phagotrophic particles); all are considered fundamental in the development of a HAB community (Burkholder et al., 2008; Sunda, 2006; Tang et al., 2010). Although we lack sufficient information to prioritize the relative impacts among these nutrients, it is realistic that most near-term HAB research will largely focus on the effects of macronutrients (and their forms) due to the intrinsic difficulties of trace-metal work (both experimental and field sampling) and in the study of mixotrophy and their prey species (Flynn et al., 2018).

Changes in runoff and increased chemical weathering will affect the magnitude, relative ratios, and availability of dissolved and organic forms of silicon, nitrogen, phosphorus and carbon. There have been considerable efforts to determine whether, or how, the availability of multiple nitrogen forms (or substrates) affect HAB species or their toxicity (e.g., Auro and Cochlan, 2013; Davidson et al., 2012). Nutrient substrates of a given element are not considered 'equal' by phytoplankton. For example, common nitrogen substrates (ammonium, nitrate and urea) may differentially affect the growth and toxicity of HAB species, including both dinoflagellates (e.g., Dyhrman and Anderson, 2003; Flynn et al., 1996; Levasseur et al., 1995) and diatoms (e.g., Howard et al., 2007; Radan and Cochlan, 2018; Thessen et al., 2009). Moreover, the dominance of these nutrient species may change in abundance as climate change affects the nitrogen cycle (Capone and Hutchins, 2013; Hutchins et al., 2009). Even so, the level of current evidence that particular nitrogen substrates enhance HAB development or cause changes in cellular toxicity is insufficient for broad extrapolations.

How these changes may influence the competitive success of HABs will depend in large part on their influence on nutrient uptake kinetics, but the uptake kinetics for N, P (and Si for diatoms) are not sufficiently understood to predict differential responses of HAB versus non-HAB species. Moreover, it is unknown whether or how climate-mediated changes in the abiotic environment (e.g., pH and temperature) will alter these kinetic parameters. Regardless, it will be useful to treat nutrient uptake kinetics as a "response variable" that will inform of the potential reaction of cells and plankton communities to climate drivers.

No single relationship between toxin content and nutrient availability or forms has been found for all HAB species, or even within genera, although some individual relationships have been observed (Fehling et al., 2004; Hattenrath et al., 2010; Leong et al., 2004; Radan and Cochlan, 2018). Just as the chemical formulation of toxins are remarkably diverse, toxin production is not a synonymic physiological response within present HAB species. The challenge then will be to determine whether a subset of general patterns exist, as suggested by Van de Waal et al. (2014), or if these relationships will necessarily have to be determined on an individual basis.

While coastal zones are more susceptible to large changes in nutrient supply, open ocean environments should not be neglected. Climate change will affect surface water nutrient regimes of the open ocean due to warming and increased stratification (N↓), changing winds (N↑↓), changing current velocities (N↓↑) and eddy kinetic energy (N↑↓). In coastal zones, any changes in precipitation regimes, storm frequency, and intensity will alter the flux of suspended sediments and dissolved catchment components (POC and DOC), along with the inorganic drivers of cell growth (N, P and Si) to nearshore waters. Warming and acidification may increase the weathering of bottom sediments and nutrient recycling rates, and thus the flux of nutrients to the water

column. These changes may also be exacerbated by localized changes in human pressures within watersheds (i.e., the component of global change—see www.igbp.net), and separating these effects will be necessary when comparing climate effects among "natural" and local culturally-altered ecosystems.

Despite the inexact understanding of the linkages between climate, nutrients, and HABs, climate-driven changes in nutrients are expected to have wide-ranging consequences for phytoplankton production overall, and potentially for HABs. There are clear linkages between nutrient flux (mainly anthropogenic production of phosphates and waters associated with agricultural operations) and many freshwater HABs, but the same is not true for most marine HABs. As such, it is not possible to generalize a universal response of HABs to anticipated climate-driven changes in nutrient flux at this time (i.e., 'no one size fits them all' strategy to describe all HABs). Still, there are three rational predictions:

1) any increase in nutrient flux to surface waters would escalate biological oxygen demand that, in turn, may promote harmful species that are resilient to low O_2 conditions (e.g., Noctiluca sp.; Gomes et al., 2014; major cyanobacterial bloom taxa, Paerl and Otten, 2013).
2) changes in nutrient availability may influence natural species assemblages (changing growth rates, physiological tolerances, competitive advantages) in ways that enhance or diminish HABs.
3) changing physical parameters (e.g., temperature, salinity, pH) may influence cell physiology and thus nutrient uptake kinetics, thereby alter the competitive interactions among species.

The broad hypothesis that climate-driven changes in nutrient supply will influence the prevalence of future HABs is too simplistic. The hypothesis unrealistically constrains a divergent problem (complex scenarios) to a convergent (single) answer. Rather, the important question is whether (and where) projected increases in nutrient flux to surface waters from altered weathering and runoff will be sufficiently large to generate new, or intensify existing, high biomass HABs, or where smaller increases, or decreases, in macro- or micro-nutrient flux or cycling can give toxic HAB species a competitive advantage over non-toxic phytoplankton. Downscaled regional components of global climate models should be used to estimate changes in terrestrial nutrient flux to coastal waters with the goal to identify regions that likely will experience the most dramatic changes, thereby highlighting priority sites for focused study of high biomass HABs. The hypothesis that toxic HABs are stimulated by nutrient conditions currently is an active topic of research, but progress is frustratingly slow because the complexity of interactions presents no unified findings. More tractable hypotheses would focus on the increased competitiveness of HAB species as defined by the differences in macro- and micro-nutrient uptake kinetics among HAB species and regionally co-occurring non-HAB species, and the effects of light, temperature, salinity, pH and other factors on these competitive outcomes. That is, delineate the reaction space where nutrient changes enable toxic species to more likely dominate, or at least become a major component of the phytoplankton community (for methods of approach see Boyd et al., 2018). The vast number of species and culture experiments this approach entails means it may be better to focus on a subset of HAB species chosen through risk assessments. These quantitative data are necessary to parameterize models that can better inform on how future changes in nutrient flux may alter the competitive success of HAB species.

7. Benthic HABs

Benthic HABs (BHABs) comprise proliferations of certain harmful species that have a dominant life history stage associated with benthic surfaces (macrophytes, algal turfs, rocks, sand, coral rubble, etc.) to which they attach by synthesizing mucilaginous substances. Due to internal physiological rhythms combined with water motion, cells can release from the benthos and become part of plankton communities as free-swimming cells or within floating aggregates. The main taxa causing harmful events are *Gambierdiscus* and *Fukuyoa* (both associated with ciguatera fish poisoning, CFP), *Ostreopsis* (related to food-borne poisonings, respiratory and cutaneous irritations in humans and massive mortalities of certain benthic organisms), *Prorocentrum lima* (producing diarrhetic shellfish toxins) and *Lyngbya* (cyanobacteria associated with clupeotoxism and skin rashes/lesions, respectively) (e.g., GEOHAB, 2012). While BHABs have traditionally impacted tropical areas, recent data suggest that these organisms are increasing their biogeographic distribution towards more temperate waters (e.g., Rhodes, 2011; Rodriguez et al., 2017; Tester et al., 2014), constituting a potential expanding global problem. This expansion, as well as observed phenological changes in benthic blooms (e.g., Nakada et al., 2018), are believed to result from climate drivers. As documented in Tester et al. (2019, this issue), several research questions and methodological challenges need to be addressed to characterize the present and future spatio-temporal trends of BHABs. Three main climate-related drivers have a strong potential to influence benthic HABs: increasing temperature, direct and indirect benthic habitat alterations, and potentially the longer-term effects from increasing ocean acidity. Higher temperatures may increase the maximum latent growth rates and toxicity of benthic HAB species (Ballantine et al., 1988; Morton et al., 1992; Pistocchi et al., 2011; see also Tester et al., *submitted*; Xu et al., 2016) as well as facilitate poleward range extensions (Rhodes, 2011; Shears and Ross, 2009; Tester et al., 2010). On the other hand, it is conceivable that future temperature maxima at low latitudes may begin to exceed the thermal tolerance of benthic HAB species (Accoroni and Totti, 2016; Kibler et al., 2012; Tawong et al., 2016), leading to their diminished biogeographic distribution in some regions. Increasing global temperatures also may affect the temporal occurrence of BHAB events, resulting in microalgae proliferation earlier in the season and along with sudden decreases in abundances as a consequence of extreme storm events (e.g., Meroni et al., 2018).

Coastal benthic habitats, both low latitude and temperate rocky reefs, have increasingly suffered degradation over recent decades (e.g., Birkeland, 2018; Castorani et al., 2018, and references therein). Many of these changes can be attributed to direct human activities—cultural eutrophication, sedimentation, over-fishing, harbor construction—but climate drivers have the potential to accelerate habitat alterations through increased frequency and intensity of precipitation, runoff erosion, and large storm events (Pachauri and Meyer, 2014). In most cases, these alterations include loss of relevant habitat forming species (corals, canopy forests) and the shift to less structured communities (algal turfs), which often facilitate colonization by benthic organisms including harmful microalgae (Catania, 2017; Chinain et al., 2010; Meroni et al., 2018). A direct link, however, between the expansion of macrophyte distributions and BHABs cannot be drawn yet based on the available data (e.g., Mangialajo et al., 2017; Yong et al., 2018).

The potential direct effects of ocean acidification on BHAB occurrences are not known. Climate driven increases in coastal acidification might increase the growth of warmer water benthic HAB species by increasing dissolved pCO_2 and reducing the need for CCMs. However, field experiments on thermal CO_2 vent regions in the Mediterranean showed that *Ostreopsis* communities in these low pH environments lack any particular response compared to communities growing in nearby unaffected areas (Di Cioccio et al., 2014). It is unclear though whether this is a universal response for all *Ostreopsis* strains let alone other benthic HAB species.

Ocean acidification also may influence BHABs indirectly by inducing changes in the substrate. Climate-driven enhancement of terrestrial runoff will increase phytoplankton production and organic matter inputs, with the resultant respiration increasing coastal acidification (Gledhill et al., 2015a). Increased nutrient flux may accelerate stress on coral communities, enhancing the likelihood of generating substrates

that are more easily colonized by benthic microalgae. Increased pCO_2 also may enhance macrophyte growth (through the reduced need for CCMs), further increasing substrate area for BHAB organisms. However, lower pH may negatively affect calcified macroalgal substrates, such as genera of the Corallinales that are known to support high abundances of benthic dinoflagellates (Blanfuné et al., 2015; Meroni et al., 2018; Vila et al., 2001). In this case, BHAB blooms could decrease. But the consequences of a novel niche opening are unpredictable. The net effect of acidification on BHAB abundance is therefore unknown, and may differ among coastal locations and habitats, but it likely is at least as problematic for BHABs as it may be for planktonic species (Flynn et al., 2015)

A major impediment to developing testable hypotheses relating BHABs to climate change is the fundamental challenge of gathering empirical data on HAB cell abundance and corresponding climate-driven dynamics in coastal systems. The first priority is to develop methods that adequately estimate BHAB species abundance per unit benthic substrate (weight or surface, e.g. Yasumoto et al., 1979), but this task is exceedingly difficult given the range of possible substrates in an area. Tracking cell abundances in the water column is feasible, but these abundances are imprecise and highly variable due to a combination of hydrography circulation patterns, turbulence and diurnal cell vertical migrations (associated to floating mucilaginous aggregates or not; e.g. Faust and Gulledge, 1996; Vila et al., 2008). Attachment to substrates allows cells to remain for longer periods in an area, generating more consistent temporal trends in abundance (Totti et al., 2010). Although sampling natural substrates is a preferred method for detecting the presence and blooms of harmful organisms, this approach faces several technical difficulties, including diverse substrate preferences exhibited by BHAB organisms (Aligizaki and Nikolaidis, 2006; Meroni et al., 2018; Parsons et al., 2012; Parsons and Preskitt, 2007; Totti et al., 2010; Vila et al., 2001), intrinsic patchiness of these benthic substrates (with inconsistent distribution in time and space), and problems in estimating substrate surface area (especially in the case of macrophytes with highly ramified morphologies) or weight without destructive sampling (e.g., sediments vs. corals, etc.). These challenges have stimulated alternative sampling strategies: increased replicate sampling (Lobel et al., 1988), artificial substrates (Jauzein et al., 2018, and references therein; Jauzein et al., 2016; Tester et al., 2014), and integrated water column sampling (Mangialajo et al., 2017). The international community must adopt an accurate, standardized method for estimating cell abundance to enable comparisons among regions and mechanistic linkages to human health impacts (Berdalet et al., 2017; GEOHAB, 2012; GlobalHAB, 2017, https://unesdoc.unesco.org/ark:/48223/pf0000256055, www.globalhab.info).

The second research priority is establishing rationales for abundance thresholds definitions of BHABs in the context of both climate change studies as well as for management of their impacts. In the case of *Ostreopsis* in the Mediterranean, experience over the last decade (e.g., Giussani et al., 2017; Jauzein et al., 2018, 2016; Mangialajo et al., 2017) has led to establishing monitoring for alert status (initiated at 30×10^3 cells L^{-1} of seawater) and emergency status (for values greater than 100×10^3 cells L^{-1} of seawater). As macroalgae form ecological habitat of the BHAB species, monitoring of the habitat density is also established with a "bloom" and a "major bloom" at 200×10^3 and 1000×10^3 cells g^{-1} of habitat-forming macroalga, respectively. These seasonal blooms occur mainly during the summer and fall (Accoroni and Totti, 2016, and references therein; Mangialajo et al., 2017; Totti et al., 2010). But the concept of "bloom" is more difficult to define in low latitude, low seasonality environments, and particularly with *Gambierdiscu,* because peaks in cell abundance may be more evenly distributed throughout the year (Chinain et al., 1999). Nutrients, temperature, salinity, light regimes and suitable substrate availability combine to determine *Gambierdiscus* growth rates, linked or not to toxin production, within the "hot season" (Kibler et al., 2012), although these benthic species may persist throughout the year.

Complicating matters, the measurement of the abundance of *Gambierdiscus* may be of limited use in forecasting effects on human health as cellular toxin content does not correspond with ciguatoxin in the food web level consumed by humans. The critical challenge then is to develop efficient, reliable and cost-effective methods for toxin detection as well as understanding how environmental factors influence toxin production by these harmful species.

Three guiding hypotheses will help to structure the assessment of climate change effects on BHABs: 1) climate drivers stimulate greater growth and toxicity of BHAB species, 2) climate drivers alter shallow benthic (bio)substrates in ways that benefit the proliferation of BHAB species, and 3) the integrated effect of climate drivers affect the biological (and chemical) pathways of toxin accumulation and transformation in the food web in ways that increase their harmful impacts. More so than for most other HAB syndromes, greater clarification of benthic HAB taxonomy is needed through microscopic and molecular techniques to support physiological studies. Fundamental questions remain surrounding the present-day factors influencing toxin production, substrate preferences, species behavior, benthic release and spreading, and life cycles (which are poorly known for most of these species); studying the effects of climate drivers may help accelerate the basic understanding of these processes. How climate drivers will shape future structures and compositions of benthic substrates are active areas of research in other fields but selecting several "standardized" substrates to study HAB species preferences would provide valuable datasets to support modeling experiments under different global benthic response scenarios. Similarly, experiments under controlled conditions on toxin transfer, accumulation, and transformation in fisheries-related species would enable preliminary parameterization of these complex processes in the rapidly evolving field of ecosystem modeling.

8. Cyanobacterial HABs

Cyanobacterial HABs generally are associated with fresh to brackish water environments, although blooms of *Trichodesmium* sp. and *Lyngbya* asp. in saline tropical and subtropical waters are considered harmful in most Asian and South Pacific nations. The cyanobacterial HABs in marine and freshwater bodies are worsened by elevated anthropogenic nutrient loading that can be the consequences of regional or local patterns of land use and population density (Burford et al., 2019; Paerl et al., 2018). Separating the effects of such localized anthropogenic pressures from those associated with climate change will be particularly challenging in the study of cyanobacterial HABs, perhaps more so than for any other types of HAB (Huisman et al., 2018).

There are clear indications that cyanobacterial HABs are enhanced by elevated temperature (O'Neil et al., 2012; Paerl and Huisman, 2008; Paerl and Paul, 2012; Suikkanen et al., 2013), so patterns of global temperature change may lead to more intense and geographically expanding cyanobacterial HABs if all other conditions are suitable (Chapra et al., 2017; Kosten et al., 2012; Taranu et al., 2015). Similarly, elevated pCO_2 leads to increased growth rates of cyanobacteria, suggesting that this climate driver also will enhance these HABs (Verspagen et al., 2014; Visser et al., 2016). But excess inputs of N and P, relative to Si, are a major driving force shifting production from eukaryotic (especially diatom) to cyanobacterial production (Paerl and Otten, 2013), and internal loading of phosphorus together with decreasing N:P ratios may enhance blooms of nitrogen-fixing cyanobacteria over other phytoplankton in some areas, such as the Baltic Sea (Vahtera et al., 2007). While increasing temperature and pCO_2 may act to exacerbate cyanobacterial HABs in regions currently experiencing them, climate drivers affecting nutrient flux to surface waters may have a dominant role in expanding the intensity and distribution of cyanobacterial HABs (*cf.*, Rigosi et al., 2014). In particular, increased variability of precipitation patterns will affect runoff intensity and the flushing/residence times of water within systems, working to either increase or decrease nutrient loading. Changes in runoff also will alter

inputs of dissolved organic matter (DOM) which may alter in-situ light fields (Creed et al., 2018) as well as trace metal nutrition (see in Gledhill and Buck, 2012) with either beneficial or negative effects (Paerl, 1988). In some cases, decreased runoff may lead to salinity increases that can restrict cyanobacterial growth. In contrast, the decreased salinities stemming from increased runoff likely will favor cyanobacteria growth in freshwater and brackish water systems. Two of the three main genera forming cyanobacterial HABs in the Baltic Sea (*Aphanizomenon* and *Dolichospermum*) originate from freshwater systems and show enhanced growth at lowered salinities (Brutemark et al., 2015; Kuosa et al., 2017; Suikkanen et al., 2013).

Developing better forecasting skill for how cyanobacterial HABs respond to climate drivers depends on several avenues of research. Although the relationships between land use, nutrient loading, freshwater discharge and the development of cyanobacterial HABs are recognized, these need better quantification and linkage to the proliferation and persistence of these HABs. The relative importance and roles of nitrogen, phosphorus, silicon, iron (Molot et al., 2014) and other trace metal inputs need to be assessed, along with the optimal thermal and light regimes and flushing rates (i.e., water residence time), and all these then coupled to explain the dynamics of cyanobacterial HABs (Huisman et al., 2018; Paerl et al., 2018). The relevant spatio-temporal scales of interactions between these drivers and cyanobacterial HAB responses also are not well understood, most likely because the drivers themselves are interactive (e.g., freshwater discharge, residence times, nutrient loads). Although much research has converged on the cyanobacteria HAB species, there needs to be more emphasis placed on quantifying the ecophysiological mechanisms involving other microbial and biotic associations that affect bloom development, persistence and toxin production (Huisman et al., 2018; Paerl and Millie, 1996).

Several model systems are potentially well suited for focused research on the effect of nutrient and climate drivers will have on future cyanobacterial HABs (Chapra et al., 2017; Hellweger et al., 2016). In the marine/brackish water realm, the Baltic Sea presents a robust system with recurrent extensive blooms of nitrogen-fixing cyanobacteria in a continuum of freshwater to coastal marine salinities exhibiting all stages of eutrophication, from highly eutrophic to less or not-yet eutrophied regions (HELCOM, 2018). A number of well-studied freshwater systems offer complementary opportunities, including newly developing reservoirs, re-eutrophicating systems such as Lake Erie, and hypereutrophic systems such as Lake Taihu (Bullerjahn et al., 2016; Michalak et al., 2013; Paerl, 2016). These geographically constrained systems are amenable to field studies that characterize the distributions of biomass and diversity in time and space, and nutrient utilization kinetics and growth rates as a function of climate-related drivers. In some cases, these constrained systems may contain sub-regions suitable for field-manipulation experiments needed to test hypotheses.

The observed correlations between increasing temperatures and the expansion of fresh and brackish water cyanobacterial blooms is perhaps the strongest signal to date of climate linked impacts on a HAB syndrome, but it would be wrong to accept this trend as predictive; many warming surface waters are not experiencing increased cyanobacterial HABs. By implication then, direct temperature effects on cyanobacterial physiology cannot be the only driver responsible for their apparent competitive success. Instead, the tight coupling of cyanobacterial production and terrestrial processes means that climate effects likely will be regionally restricted and dependent on indirect drivers associated with increasing temperature. Given that the positive relationship with temperature is observed in both marine and freshwater systems, hypothesis testing should focus on the subset of uniform principles that are applicable to both environments. There should be particular emphasis to distinguish the forcing by climate drivers from those associated with localized anthropogenic nutrient effects. In addition to testing hypotheses in well-controlled laboratory experiments, researchers should exploit the fact that many cyanobacterial HABs occur

in geographically and hydrodynamically constrained systems that are tractable to focused studies that test climate driver effects. As ongoing efforts to downscale global climate models to regional scales begin to mature, it seems likely that forecasting skills could advance faster for cyanobacterial HABs than for other marine HABs (Chapra et al., 2017).

9. Grazing and HAB dynamics

The narrow insight to specific planktonic predator-prey interactions in coastal waters means that grazing effects on HAB dynamics remain one of the more vexing problems facing HAB scientists. Grazing can regulate phytoplankton biomass, but the extent to which grazing pressure, either species specific or general, enhances or diminishes the relative abundance of HAB species is unclear. As discussed in Wells et al. (2015), there appears to be no unifying physiological or ecological features of HABs that set them apart from other phytoplankton species with respect to grazing, although there is emerging evidence that in some cases toxins appear to inhibit grazers. For example, copepods appear to display selective aversion to *Alexandrium* spp. cells containing PSP toxins, influencing their grazing activity (Colin and Dam, 2004; Dam and Haley, 2011; Teegarden, 1999). Similar decreases in copepod grazing rates associated with *Karenia brevis* are thought to be due to its toxicity (Hong et al., 2012; Waggett et al., 2008), although it also may be related to its nutritional inadequacy (Waggett et al., 2012). There are few studies to assess whether these findings apply more broadly to toxic HAB-grazer interactions. Alternatively, there are circumstances where grazing pressures may drive HAB organisms to form more concentrated HAB formations; for example, predation can drive the euryhaline *Heterosigma akashiwo* to take refuge in low salinity surface plumes (Strom et al., 2013). Given the projections for more intense episodic precipitation events under future climate change, is it reasonable to expect increased frequencies of these HAB-facilitating oceanographic conditions? Conversely, the development of harmful *Noctiluca* blooms relies upon the successful growth of its phytoplanktonic prey (e.g., Gomes et al., 2014; Lotliker et al., 2018), so will more general forecasts for changes in phytoplankton production help inform on the future of these HAB events? In a similar vein, as already mentioned, mixotrophy is common among many dinoflagellate species (Flynn et al., 2018; Stoecker, 1999), but are there conditions where HAB mixotrophs outcompete non-HAB mixotrophs, thereby enhancing HAB development? For example, *Prorocentrum micans* decreases its CO_2 requirements when it turns from autotrophy to mixotrophy (Jeong et al., 2016)—will ocean acidification influence this shift, and if so will it be due to physiological changes within *P. micans* or to OA impacts upon its prey (Flynn et al., 2015)? Add to this complexity the potential for grazing cascade effects, whereby selective feeding by mesozooplankton or higher trophic levels alters the microzooplankton grazer ecology to increase or decrease grazing pressures on HAB species. Even so, many toxic HAB blooms do not require high biomass—PSP events can develop with cell abundances as low as a few hundred cells per liter (e.g., Maine Department of Marine Resources)—so does grazing have little role in regulating the occurrence (vs. intensity) of these types of HABs? Overall, there is a lack of hard data on predator-prey interactions, and experiments suitable to provide the critical rate measurements are needed for quantifying grazing impacts.

Addressing these questions in the context of climate drivers remains daunting. We lack a basic understanding of the zooplankton distribution across the size spectrum associated with HAB events, let alone evidence of mechanistic linkages between grazing and HAB development. Are there good proxies for quantifying grazing rates during HAB events that do not require knowledge of the complexities underlying these processes? What tools or approaches can be developed to help quantify these fundamental rate processes? But there are opportunities to study subsets of the grazing issue. One example relates to euryhaline tolerance of *Heterosigma akashiwo* which can lead to reduced grazing pressure (Strom et al., 2013). Are there other examples where changes

in these or other oceanographic "refuges" may shape how climate drivers influence grazing pressures on HABs in the future?

Beyond potential changes in oceanographic refuges, the consequences of changing climate drivers for grazing processes can be envisioned within two broad categories; changes that help to select for, sustain, or enhance the growth of HAB species (e.g., nutrient-stress driven transitions to mixotrophy by HAB species, the selective grazing on HAB species competitors), and those that restrict HAB development (increased grazing pressure on HAB species, or the phytoplankton community in general). Testing independent and combined climate driver effects on HAB mixotrophy and selective grazing by micro/mesozooplankton are very amenable to laboratory experiments and would provide the fundamental quantitative insights needed for model development. In contrast, hypothesis testing of climate driver effects on top-down grazing pressures in complex, full plankton communities will be more logistically (and financially) challenging because larger scale (i.e., mesocosm) experiments likely are needed to capture the complexity of interactions. In parallel with these studies, and informing their experimental design, quantitative models should be developed specifically to investigate grazing impact scenarios on HAB development. These modeling efforts will be particularly important given the complexities of simultaneous bottom-up and top-down controls of HAB species, and the broader phytoplankton communities. However, with few exceptions (e.g., Collumb and Buskey, 2004; Olson et al., 2008; Turner and Tester, 1989) there are very limited data on grazer interactions during HAB events, and in general terms, zooplankton model development lags far behind that of phytoplankton (Mitra et al., 2014a). There is an acute need for new and quantitative insights to stimulate progress in understanding climate driver influences on HAB/grazing dynamics.

10. Fisheries, aquaculture, and HABs

Although the term "harmful algal bloom" has evolved to include a broad array of ecological impacts, the major concern arguably remains that climate drivers may intensify threats to human health through magnifying HAB impacts on fisheries and aquaculture (Barange et al., 2018). New experimental strategies are needed to study not only how climate-scale processes could generate local stresses that stimulate HAB occurrences, but also how best to distinguish local-scale human influences from those driven by a shifting climate. Beyond the study of the potential for HAB expansion, what can be done to address concerns about future HAB effects on fisheries and aquaculture?

The normal, constrained strategies of HAB monitoring to focus on HAB species and toxin measurements should expand to sample whole phytoplankton communities, and at least a suite of basic oceanographic parameters, to build datasets on HAB ecophysiologies that can better inform and improve management practices. These monitoring programs should include estimations of toxic species as a proportion of the overall phytoplankton biomass, and specific or broad spectrum assays that would allow for the detection of new toxins, including toxins that do not affect humans but negatively impact the health of other organisms such as shellfish. Many agencies have developed sensitive chemical and cell-based assays to replace animal bioassays, so it is now possible to detect trace levels of toxins and employ screening for novel toxins (Reverte et al., 2014; Turner et al., 2015). This effort will alert agencies to the background emergence of any new toxins in advance of them causing any health problems or economic hardship. In a departure from normal procedures, monitoring should continue year-round, albeit at a reduced effort in "off-seasons"; transitions from "off season" conditions may have an important role in regulating the extent of subsequent HAB development (e.g., McGillicuddy et al., 2011). Although these added tasks will be beyond the realistic limitations of many monitoring programs, it should be possible to focus on a limited number of geographically-distributed sentinel sites covering wild and aquaculture harvesting regions. Some of these should be located in climate hotspots

(Hobday et al., 2016). Extensive shellfish toxin monitoring programs with decades of historical data can be found in the Gulf of Maine (Shumway et al., 1988), the Salish Sea (Trainer, 2002), along the Irish coastline (McPartlin et al., 2017, and references therein), in the United Kingdom (Hinder et al., 2011), in Japan (Fukuyo et al., 2002), and many other locations worldwide (Wright, 1995), most of which have access to at least some regional oceanographic datasets. Although many of these datasets likely been utilized for developing short-term (monthly, seasonal) forecasts of HAB development, they could help provide the data richness essential for resolving longer-term trends in past HAB occurrence (e.g., Hallegraeff, 2010; McCabe et al., 2016). Similarly, fish aquaculture sentinel sites should span wide geographic and latitudinal ranges, including net-penned fish aquaculture in South Korea, the Salish Sea in British Columbia, Canada, and the fjordic Chilean, Norwegian and Scottish coastlines. For those mixotrophic species specifically reliant upon certain prey (Mitra et al., 2016)—the specialist non-constitutive mixotroph HAB *Dinophysis*, being the most obvious example (Hansen et al., 2013)—monitoring prey for HABs also is important.

What steps might be taken now to help reduce or minimize the potential economic, cultural, and human health effects from HAB-affected fisheries and aquaculture? One approach should be to explore the types of fish or shellfish for species that can be cultivated in higher-risk regions but are more resistant to, or accumulate less, HAB toxins. Mitigation of high-biomass HABs triggered by anthropogenic nutrient inputs is conceptually straightforward—limit the flux of nutrients to the region—but approaches to mitigate the development or persistence of toxic HABs remain enigmatic. Although clay dispersal has proved successful in controlling *Cochlodinium polykrikoides* blooms in Korea (Seger et al., 2017), it has the potential for significant detrimental effects on filter-feeding invertebrates (Shumway et al., 2003). But the concentrations necessary to mitigate HABs are reported to pose no threats on aquatic organisms (Yu et al., 2017, and references therein). Strict environmental controls, however, have prevented the use of this approach in other nations. Exploring the possibility of using more targeted bloom control strategies (e.g., amendments with grazers, toxins, viruses; summarized in Anderson et al., 2015) could be useful, but this research or practice is difficult or outright banned in some countries (e.g., USA). Investigations on more holistic approaches to toxic HAB mitigation, such as restoration of coastal habitats with seagrass that harbor algicidal bacteria (Inaba et al., 2019) should be a high priority given the potentially broad implications for the human dimension.

The hypotheses that climate drivers will exacerbate marine, brackish and freshwater HABs emphasizes the need to develop short term [e.g., extreme event—McCabe et al. (2016)] and longer-term (decadal trends) fisheries forecasting capabilities to inform managers, stakeholders, and the public. Methods to provide short-term early warning of likely location and magnitude of HABs are of great value to the aquaculture industry, informing business planning and ensuring the protection sustainable fisheries and human health. These forecasts allow industry to expedite or delay harvesting of shellfish to avoid toxicity issues or undertake measures to protect farmed fish (e.g., the deployment of tarpaulins or bubble curtains). Similarly, early warning will allow managers to anticipate and mitigate directs effects of non-conventional HABs on shellfish health (e.g., yessotoxins; De Wit et al., 2013) The building blocks for such systems are in place in those regions (e.g. western Europe, U.S.A.) having well-developed shellfish biotoxin and plankton monitoring programs, satellite based remote sensing data, pre-existing hydrodynamic data, and coastal ocean observatories (Barth et al., 2019; Davidson et al., 2016). Longer-term forecasts of climate-altered HAB probabilities, akin to long range weather forecasts, should be developed now using a range of potential climate settings. These forecasts would be useful, not as prescriptive tools, but as scenario-based tools for investigating, and informing, on prospective outcomes.

11. HAB modelling

Improved HAB modeling skills are prerequisite for understanding how climate and environmental drivers may influence future HAB events. There is a role for different types of models (i.e., statistical, simulation or mechanistic) and the scale on which they may be operated. Model types range from representations of cell physiology (e.g., linking nutrient status to toxin content) that increase a species environmental scope or ecological resilience, to representations of different species and predator-prey combinations for theoretical and conceptual exploration of conditions conducive to HAB development (Flynn and McGillicuddy, 2018; Franks et al., 2018). Although regional or local scale models arguably may be most useful for the operative understanding of short and long-term ecological and human consequences, working at these scales remains challenging because even the most detailed physics representations only recently are achieving the grid scales (ca. 250 m) required for effective coastal zone models. Regional scale models will need to be informed by global scale models to fully capture climate change impacts in future scenarios. Simulation models operated in conceptual settings could provide platforms for exploring more generic issues affecting HAB dynamics; notably in this context is the increasing awareness of the importance of mixotrophy in these organisms (Flynn et al., 2018), which may warrant a general revision of how HAB research is conducted.

Although most current global ocean models incorporate phytoplankton, with more sophisticated simulations parameterizing different groups of phytoplankton (e.g. diatoms vs. flagellates, large vs. small; Follows et al., 2007), HAB modelling will require developing modelling frameworks and skill for projecting how individual species compete against one another for limited resources. More problematic are the issues of mixotrophy and the selective grazing on HABs (e.g., Mitra et al., 2016). Taken together these present significant challenges to plankton science and will require a multidisciplinary proactive approach to ensure progress in a timely fashion. Linkages must be developed among laboratory workers, physiologists and biochemists working with modelers to help develop, test and apply systems–biology models. Additional exchanges are required between these groups and field researchers with their modeling counterparts (ecosystem modelers). Promoting these interdisciplinary dialogues is not a simple process, but can be achieve through the formation of expert groups that include modelers with specific expertise (e.g., Mitra et al., 2014b). The importance of such dialogues not only is for improved scientific understanding but also to help ensure that modellers do not extract information and concepts from the literature without critical oversight of the general value, or limitations, of such information. The reverse also is true, whereby input from modellers will help experimentalists and field scientists shape laboratory and field studies to provide the key parameterization that is needed for model refinement.

Managing expectations will be imperative, as it must be acknowledged that our current fledgling steps lie far from creating a true forecast capability for HABs based upon dynamic models [as distinct to combining statistical models with field sampling; e.g., Anderson et al. (2013) and Flynn and McGillicuddy (2018)]. This does not mean that current dynamic models are not of value, because at the least they can help identify general combinations of conditions that may be conducive to the establishment (or diminishment) of HABs (Lin et al., 2018). Such models would have clear roles as aids in general aspects of environmental management (Asnaghi et al., 2017). It is, however, difficult to *forecast* future events if we do not understand (i.e., cannot successfully model) the key controls of present events. As detailed above, improved understanding is needed of the interactions between organisms, among their groups (prey, predators, competitors), and with the environment (nutrient concentrations/types/ratios, light, temperature, pH, salinity etc.). It should then be possible to improve both the statistical and mechanistic linkages between environmental drivers and different types of HAB events. These models can explore whether such events may become more or less likely at given geographic locations under climate change conditions. In this context, it also is important to recognize the challenges in plankton monitoring work, and that the study and survey of mixotrophic species relies on tracking critical prey species as much as that of their mixotroph predators (Hansen et al., 2013; Leles et al., 2019, 2017).

Developing successful ecological models necessitates identifying the minimum (functional) trait combination required, balanced against the need for useful discriminating traits and computational load. We should parameterize only the subset of drivers that are sufficient in number and relative importance to capture the response of the whole system. However, a major challenge is the identification of *traits of consequence* that define HAB species and, critically, those for co-occurring non-HAB species. HAB events only result when activity of competitors and predators allows their proliferation; i.e., we can only model such conditions with knowledge and incorporation of all the major players. Herein lies a problem in HAB science; there are only scant data relating HAB species existence to other organisms they encounter in nature—data that are essential to formulate dynamic models. There also are important life history and behavioral traits (notably cyst formation and mixotrophy) that are typically absent from model descriptions (Azanza et al., 2018; Lee et al., 2018).

A key priority in HAB modeling will be to identify the biggest model uncertainties, a non-trivial task not least because only correctly structured models offer a route to locating factors that exert greatest leverage on behavior. However, certain features of models can be identified now as being structurally questionable. Notably these include features relating to grazing and prey-switching (Flynn and Mitra, 2016), and in general terms to zooplankton growth and activity (Mitra et al., 2014a); blooms (by whatever definition) can only develop if grazing pressures are low, or if this predatory behavior selectively removes competitors (Irigoien et al., 2005). Identifying chemi**co-**physical features that diminish the potential for HABs to develop or to speed their disappearance warrant exploration. However, as noted earlier, understanding just the autecology of the HAB species can only ever represent a fraction of the knowledge required. It is important that information relating to other components of the planktonic (and as appropriate, benthic) food web be available.

12. Key species/strains for focused HABs/climate change research

The astonishingly rapid advances in biomedical research over the past two decades stems to a significant extent from utilizing a single, non-human model system; *Drosophila melanogaster*, the common fruit fly. HAB scientists should take a similar approach by selecting a very small subset of key HAB species representative of high biomass HABs (including cyanobacteria), pelagic toxic species, and benthic toxic species for more focused research efforts and thence accelerate progress on assessing climate driver effects. The lessons learned by these concerted efforts would, in turn, help to identify specific research priorities for escalating studies with a broader range of species among HAB categories. This approach would be particularly valuable for molecular studies, as still is the case for *Drosophila*. Several genera (including in turn different toxic and non-toxic species) that could be considered for selecting this small subset include *Dictyocha, Dinophysis, Alexandrium, Gambierdiscus, Karenia, Cochlodinium* (now *Margalefidinium*), *Prymnesium, Heterosigma akashiwo, Vicicitus* (formerly *Chattonella*), *Pseudo-nitzschia, Microcystis, Dolichospermum, Azadinium,* or *Nodularia.* The final short-list of species on which to focus molecular research should be guided by a range of criteria that include considerations of human mortalities, people hospitalized, and economic or ecological impacts. The desire to converge on particularly problematic species must be balanced by an appreciation of the difficulty in rearing them in culture. It may be that non-HAB species may prove to be more valuable than HAB species in teasing apart the general metabolic responses to climate drivers using molecular tools; metabolic responses that then can

be investigated in HAB species. Using such a reductive approach could greatly hasten advances in understanding about how climate drivers regulate the physiology, toxicity, and ultimately the competitive success of HAB species.

13. Experimental strategies, new tools, and observation infrastructures

The broad consensus among Symposium participants was that HAB scientists need to develop and utilize new experimental strategies, tools and observational capabilities if knowledge about climate driver effects on HABs are to progress faster than the development of those impacts. Many of these ideas reflect those proposed in Wells et al. (2015) but these and others were re-considered by Symposium participants in the context of specific research themes and are summarized here.

13.1. Experimental strategies—culture studies

Culture studies are the primary means to investigate fundamental aspects of HAB species in terms of toxin production, life cycles, interactions with bacteria (Brodie et al., 2017), etc., as well as their physiological (and limited ecological behavioral) responses to climate drivers. As described by Boyd et al. (2018), single driver manipulation experiments provide useful mechanistic insights, but even with scenario-based designs (i.e., selective choice and levels of drivers) single driver experiments can fail to capture threshold levels of physiological change. Embracing multi-factorial experiments is critical to fostering an integrative understanding of climate change impacts on HABs, but even a modest selection of three drivers at multiple levels becomes logistically impractical. Shifting from the traditional gradient approach of mechanistic experiments to a scenario-testing approach helps to mitigate these challenges, whereby the most relevant subset of drivers, their levels and combinations are designated to create a collapsed experimental design representing selected future conditions. The conceptual perspectives and experimental strategies presented by Boyd et al. (2018) should become a guiding resource for the design of HAB culture experiments moving forward.

Strain selection of HAB species for study has become of greater relevance with emerging evidence of substantial variability in the response among some HAB species strains to climate drivers (e.g., Kremp et al., 2012). The use of multiple HAB species strains from within (or among) different geographic domains will provide more balanced insight to driver responses. The strategy of collaborative "Common Garden" experiments—i.e., the same experiment being conducted among laboratories each using local strains—should become mainstream within the HAB research community. Although there is great value in using widely available strains to facilitate study inter-comparisons, inclusion of additional, more recently isolated strains whenever possible will help to reduce the risk that genetic drift from long-term culture may bias experimental outcomes. Inclusion of one or more regionally relevant co-occurring non-HAB species should become the norm in published HAB studies.

Investigations are needed at intermediate scales of complexity (e.g., microcosms and mesocosms; Riebesell et al., 2018), where greater levels of physical (e.g., mixing, stratification, light fields) and biological (e.g., grazing, nutrient recycling) complexity can be incorporated into multiple climate driver scenarios. Given that HABs are a consequence of a competitive outcome within the phytoplankton assemblage, understanding the broader assemblage response to climate drivers is indispensable.

13.2. Experimental strategies—field studies

Developing conceptual and mechanistic linkages between climate drivers and HAB occurrences demands the synergy of laboratory and field studies, particularly given that observational-based field investigations of (by definition, complex) natural systems lack controls. Although many field studies center on identifying the presence/absence of HAB organisms, sometimes with basic oceanographic observations, these programs should emphasize more fully characterizing the oceanographic conditions before, during and after HAB events. Although this expansion is impractical for many monitoring agencies, cross institutional and agency collaborations should be encouraged to bridge the gap among HAB programs and nearby observing capabilities, regardless of the level of observing sophistication. Collaboration will be indispensable to ensure the observational parameters are broadened to encompass the locally most relevant climate drivers, and that the sampling frequency, methodologies and analytical protocols reflect current recommendations. For example, linkages to centers of globally distributed ocean acidification observatories (http://www.goa-on.org) are welcomed, and would couple HAB studies with expert measurements of seawater pH (Dickson et al., 2007; Riebesell et al., 2010). A more integrated communication network including regulators, fisheries scientists and aquaculture specialists could provide access to a wide range of data sets that can be studied retrospectively for potential climate-related trends. Although there is a rational tendency for researchers to site field programs in local regions experiencing HAB problems, it is a priority that HAB observational programs become established components of new and existing observatories in regions already recognized as climate "hot spots" (e.g., Hobday et al., 2016).

13.3. Experimental strategies—guidelines for best practices

The quantitative comparison of findings among published HAB studies is greatly restricted by the wide range of methodologies and laboratory culture conditions commonly employed (e.g., nutrient concentrations, light levels, temperature, pH control). The same is true among field studies (e.g., the modes, frequencies, and strategies for sampling,). Some unification of methods, to the extent possible, is needed, similar to that developed specifically for ocean acidification studies (Riebesell et al., 2010). While of critical importance for the study of some HABs (e.g. BHABs), the need to detect and quantify the inherent variability of all HAB species responses demands minimizing the dissimilarities among experimental systems. Steps are underway now to initiate community consensus on the guidelines for best practices for HABs and climate change research (http://globalhab.info).

13.4. Experimental strategies—sediment records

As with climate science as a whole, peering into the past can illuminate the future. Sediment records of cyst distributions provide a potentially rich but strongly under-utilized framework for studying some HAB taxa (Dale, 2001). Sediment cores are straightforward experimentally to obtain and study microscopically, and with the advance of HAB specific probe capabilities, genomic analyses could provide rich insights to a broader range of HAB taxa. Although past trends are not a guarantee of future responses, these trends (or presence vs. absence) can bolster or challenge current paradigms.

13.5. Experimental strategies—socioeconomic consequences

Although HAB research has evolved mainly through biological/ecological studies, its relevance is with respect to human wellbeing (Ritzman et al., 2018). The impacts then of climate driven changes in HABs on human wellbeing will be a critical component of any assessment, yet what metrics will be used? Studies of the monetary and socioeconomic impacts of HABs on fisheries are rare or fragmented, and it is not even clear how to comprehensively quantify these outcomes. The social and cultural value of fish and shellfish, especially in remote areas where these marine resources are a critical protein source, will become increasingly important in an era of climate change. The inclusion of social, traditional knowledge, and cultural studies of coastal

communities and their resilience to climate change should be an integral component of research programs that follow collaborative community research protocols. Future strategic plans should intensify efforts to develop better connections and communication to the public and other stakeholders to expand access to the current understanding and scientific thinking on the potential effects of climate change on HABs, and the implications on both national and local community scales.

13.6. New tools—molecular approaches

The broad array of poorly quantified processes affecting HABs—e.g., HAB physiological and competitive status related to the phytoplankton assemblage, the influence of mixotrophy and grazing pressures that selectively shape the assemblage—call for new tools to be adapted for HAB field (and laboratory) studies. These include the use of stable isotopes/tracers (e.g., fluorescent markers), in situ probes (e.g., nutrients), or other physiological indicators during field (bloom) studies to quantify cell concentrations, cell physiology, cell toxicity, planktonic community structure, nutrient availability, or the rates of chemical and ecosystem processes. Rapid advances in "-omic" technologies (genomics, transcriptomics, proteomics, metabolomics) offer unprecedented opportunities to revolutionize the study of HAB species and dynamics, but although their strengths for HAB research were well described some time ago (Anderson et al., 2012), there are too few studies utilizing this potential. For example, there are a lack of primers for numerous important species and, likewise, for the prey of mixotrophic HAB species. A two-phase approach is needed, with efforts being devoted to specific gene function as well as quantifying taxa for field observations. Genomic/metabolomic tools can extend standard measurements during culture studies to assess the onset and functioning of known genes (e.g., nutrient uptake, stress-related, etc.) as a function of multi-driver scenarios. There is the potential to use microarray approaches, such as now exist for N processing genes, but we so far lack these HAB-centric tools. Existing large gene banks are rich resources to begin building these and other tools to investigate the molecular underpinnings of the physiological responses of HAB species within phytoplankton communities, and thus their likely response windows to climate drivers. As pointed out by one reviewer, genomic approaches might identify species with highly conserved genomes versus those that readily incorporate new genes enabling rapid adaptation, thereby helping to guide laboratory studies as well as risk assessment of poorly predictable HAB syndromes.

Although identifying the gene regulatory networks for toxin production in HAB species is a prized target, it is proving to be a difficult one. Many other physiological indicators may be more accessible, and perhaps more valuable, for forecasting HAB responses; e.g., some genes may differently control toxin production as a function of environmental stressors. This work, along with developing species probes for quantifying presence in the field, would best proceed by encouraging strategic collaboration among laboratories to maximize research synergy and prevent duplication of efforts. Selecting a sub-group of HAB species for focused research also would further accelerate progress (see below). For the aims of identification and quantification, linkages with industry could help broaden funding sources given the likely markets for HAB specific molecular tools.

13.7. New tools—in-situ sampling

A suite of new autonomous technologies has emerged in oceanographic studies over the past decade (Fabien et al., in review), and these advances should be implemented in the study of HAB impacts on fisheries and aquaculture. These *in-situ* field technologies include Environmental Sample Processors (ESP) and other new molecular sampling technologies, microscopic instruments such as the Imaging Flow CytoBot (IFCB) and FlowCAM, as well as instrumented gliders, profiling floats, and other autonomous vehicles. But utilizing these tools to study how climate drivers may influence HABs requires more than simple observations. Instrumented gliders, profilers, and mooring arrays can provide a 4D picture of near surface water conditions to as a backdrop to developing HABs, and IFCB and FlowCAM are capable of detecting the presence of HAB species within phytoplankton communities. But what steps can be taken to use these observational methods to move beyond observation to, for example, measure *in-situ* growth rates, or the competitive interactions among HAB and non-HAB species? Combining these tools with flow cytometric-type molecular probe approaches would add great value to these observational tools as the instruments become more widely distributed. Even so, these new technologies should be used in concert with classical light microscope-based techniques, which can provide other detailed information as well as observational validation.

13.8. New tools—mitigation

If the future indeed holds progressive and accelerating increases in HAB frequency and intensity, society will be looking to science for mitigation options. Some steps already are clear—decreased anthropogenic nutrient inputs ultimately will diminish many cyanobacterial and other high biomass HABs—but there is little research on the mitigation of toxic HABs, with some exceptions (e.g., Seger et al., 2017). HAB mitigation methods are needed that specifically target problematic species but have limited impacts on plankton assemblages as a whole; a seemingly unattainable goal. But now is the time to conceive, develop, and evaluate novel schemes at trial scales. For example, biological (e.g., viral) or species-specific nanotechnology tools may prove effective at selectively targeting HAB species within phytoplankton communities, and although these invasive approaches require great caution, fish and shellfish are important sources of protein in a future world so exploring these avenues may provide critical backstops. In the case of fisheries aquaculture strategies to minimize impacts when HABs do occur, investigations into current physical methods such as enhanced flushing and aeration of cages, feeding cessation, etc. would help to optimize these and other practical steps. Although fewer choices exist for most bivalve aquaculture—toxin depuration methods are generally very expensive—there so far has been little concerted study of animal treatments that might accelerate depuration and therefore lessen HAB impacts on aquaculture. Innovative natural mitigation measures should be explored, including the use of sea grass restoration to re-balance coastal phytoplankton communities (Inaba et al., 2019).

13.9. Long term observatories

Developing compelling evidence/documentation of climate change effects on the distribution, frequency and intensity of HABs in freshwater and marine environments ultimately depends upon rigorous long-term datasets. Current efforts to develop a global assessment of changes in HABs in the recent past (Hallegraeff et al., Global HAB Status Report, in prep.) is an essential start, but the majority of past HAB records lack the necessary environmental data to test hypotheses. More comprehensive HAB/environment time series data are needed over the next decade to improve the skill of HAB models and lead the way to more reliable "weather-style" HAB trend forecasts. In most cases, augmenting existing observatories offers the most realistic and cost efficient mechanism. First, as noted above, direct or indirect linkages should be established between food safety monitoring programs and local or regional shore-based or coastal observation networks. Second, well-established observatories already exist in many freshwater and coastal and shelf marine environments (e.g., Barth et al., 2019) to record suites of physical and biological parameters (e.g., temperature, salinity, light, pH, stratification intensity, nutrients and chlorophyll) that could be augmented to measure core HAB measurements, including HAB species and phytoplankton community composition (e.g., IFCB), or toxicity (e.g., Environmental Sample Processor). The temporal frequency of

sampling should be sufficient to resolve the responses to the major drivers at both bloom and seasonal time scales. Third, these networks should span globally important aquatic habitats (lakes, estuaries, coastal oceans, the open ocean) that currently experience HABs and are believed to have a high probability for changes in HABs in the future: sentinel sites for climate change. It will be particularly important to collaborate with any new observation platforms planned for high latitude waters, where the effect of climate drivers will be magnified relative to lower latitude coastal regions (e.g., Hobday et al., 2016). Although observatories encompassing broad suites of environmental and HAB specific parameters are of obvious value, the strong merits of less comprehensive programs covering only a few parameters cannot be overstated; changes through time are the primary metrics needed.

13.10. Taking stock

The open-ended considerations here of new tools and experimental strategies to advance our understanding of climate change effects on HABs do not take into account the reality of funding resources; an intention integral to the Symposium structure so as to not constrain the participants' vision. Given the limitation of resources though, the topics presented here should be prioritized to accelerate advances in our understanding of HABs, perhaps through categorizing the major risks and then the feasibility of useful outcomes from all possible research avenues in terms of mitigation of these risks. Establishing round-table discussions on an on-going basis at bi-annual International HAB meetings would provide a useful forum for HAB scientists to consider issues, strategies, and their opinions to help collectively shape the research priorities.

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