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Climate Change and Harmful Algal Blooms: Insights and perspective

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ABSTRACT

Climate change is transforming aquatic ecosystems. Coastal waters have experienced progressive warming, acidification, and deoxygenation that will intensify this century. At the same time, there is a scientific consensus that the public health, recreation, tourism, fishery, aquaculture, and ecosystem impacts from harmful algal blooms (HABs) have all increased over the past several decades. The extent to which climate change is intensifying these HABs is not fully clear, but there has been a wealth of research on this topic this century alone. Indeed, the United Nations' Intergovernmental Panel on Climate Change's (IPCC) Special Report on the Ocean and Cryosphere in a Changing Climate (SROCC) approved in September 2019 was the first IPCC report to directly link HABs to climate change. In the Summary for Policy Makers, the report made the following declarations with "high confidence":

- Harmful algal blooms display range expansion and increased frequency in coastal areas since the 1980s in response to both climatic and non-climatic drivers such as increased riverine nutrients run-off.
- The observed trends in harmful algal blooms are attributed partly to the effects of ocean warming, marine heatwaves, oxygen loss, eutrophication and pollution.
- Harmful algal blooms have had negative impacts on food security, tourism, local economy, and human health.

In addition, the report specifically outlines a series of linkages between heat waves and HABs. These statements about HABs and climate change and the high levels of confidence ascribed to them provides clear evidence that the field of HABs and climate change has matured and has, perhaps, reached a first plateau of certainty. While there are well-documented global trends in HABs being promoted by human activity, including climate change, individual events are driven by local, regional, and global drivers, making it critical to carefully evaluate the conditions and responses at appropriate scales. It is within this context that the first Special Issue on Climate Change and Harmful Algal Blooms is published in Harmful Algae.

When considering HABs and climate change, warming has received the greatest amount of attention in the scientific literature. A requisite for warmer temperatures intensifying a HAB in a given location is the existence of temperatures below those supporting maximal growth. There are many instances where this precise scenario has already occurred, with HABs intensifying as waters have warmed closer to temperatures that yield maximal growth (Moore et al., 2009; Gobler et al., 2017; Anderson et al., 2012). There are also locales where this is predicted to occur in the future (Glibert et al., 2014). Freshwater HABs caused by cyanobacterial blooms seem to be the most obvious examples of warming induced intensification with several case studies, from nearly every continent, indicating that the temperatures yielding maximal growth rates for many cyanobacterial HABs are universally higher than those of non-harmful eukaryotic algae (Paerl and Huisman, 2008, 2009). In marine systems, warming has been implicated in intensifying multiple HABs in several mid- and higher latitude regions (Moore et al., 2009; Gobler et al., 2017; Griffith et al., 2019). Conversely, however, these regions with increasing frequencies and intensities of HABs due to progressive warming may be balanced by regions that warm beyond of the optimal range for other HABs (Griffith et al., 2019). Collectively, this leads to a scenario whereby HABs may be migrating pole-ward with progressive warming, a hypothesis that has been affirmed by several case studies within the literature (Gobler et al., 2017; Griffith et al., 2019; Hallegraeff, 2010).

HABs migrating to new ecosystems, however, may create significant risk to aquatic ecosystems and the humans who live near them. Specifically, when HABs emerge in new ecosystems, both the humans and aquatic life living within that ecosystem are taken by surprise. Naïve species, that have never been exposed to a given HAB and /or its harmful effects, may be the first to experience selective pressures and

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thus suffer the greatest population declines (Colin and Dam, 2002; Bricelj et al., 2005). In parallel, regulatory agencies and medical facilities that have not considered, monitored, and treated a newly arriving class of HAB-toxin may be taken by surprise as 'first ever' events occur, contaminating seafood, and potentially sickening people.

The root cause of ocean warming is, of course, the accumulation of CO_2 in the atmosphere that comes into equilibrium with, and acidifies, the surface ocean (Doney et al., 2009). In doing so, the higher availability of CO_2 offers the potential to rebalance the distribution and abundance of primary producers that rely upon inorganic carbon to perform photosynthesis (Giordano et al., 2005). While the net effect of rising CO_2 on phytoplankton communities is not fully understood, it has been hypothesized that since the RUBISCO found in dinoflagellates has a lower affinity for CO_2 than other phytoplankton, dinoflagellates, which cause the majority of marine HABs, are more likely to benefit from rising CO_2 levels than other classes of algae (Reinfelder, 2011). While this hypothesis oversimplifies the organizing effects of high CO_2 on phytoplankton communities, this theory is supported by a recent meta-analysis of 26 studied HABs that demonstrated growth rates increased consistently with elevated CO_2, while non-harmful algae did not show this trend (Brandenburg et al., 2019).

Regardless of how HABs respond to climate change, scientists that study HABs and managers and the public are concerned with HABs because of the harm they cause to aquatic ecosystems and their inhabitants, including humans. For more than a decade, scientists have also expressed growing concern regarding the negative effects of climate change processes on aquatic life (Gruber et al., 2011; Doney et al., 2012). Temperatures in some ecosystems are expected to reach levels that cause significant physiological stress to aquatic organisms (Pörtner et al., 2008). Concurrently, levels of dissolved oxygen in the ocean have been declining since the mid-twentieth century, and this trend is expected to continue through this century as warmer waters will hold less dissolved oxygen (Breitburg et al., 2018). Within coastal zones, hundreds of instances of hypoxia have been identified (Breitburg et al., 2018) and hypoxic zones have been expanding (Keeling et al., 2010). Ocean acidification is depressing the pH and saturation state of calcium carbonate in the ocean (Doney et al., 2009), with predicted mid-century levels of acidification representing a threat to the growth and survival both calcifying and non-calcifying organisms (Gobler and Bauman, 2016). And, this trifecta of threats (warming, acidification, and hypoxia) are already manifesting within coastal zones. Coastal heat waves have become common, bringing temperature anomalies that often exceed the end-of-century predictions (Frölicher and Laufkötter, 2018). Emerging research has demonstrated that hypoxic zones are also acidified, as the microbial respiration that drives hypoxia also produces CO_2 that acidifies water in the same manner atmospheric CO_2 does (Wallace et al., 2014; Waldbusser and Salisbury, 2014). While each of these processes are a physiological threat to aquatic life, they often occur in tandem and the co-occurrence of these stressors commonly leads to physiological outcomes additively worse than a single stressor and in some cases, synergistically worse (Depasquale et al., 2015; Stevens and Gobler, 2018; Tomasetti et al., 2018). These occurrences are typically rooted in organismal physiology as stressors may frequently act on similar or the same biochemical pathway (Pörtner and Farrell, 2008).

While the co-occurrence of climate change stressors and their physiological impacts have been well-studied during the past decade, what has been lacking has been a consideration of how the co-occurrence of one or more climate change stressors with HABs might affect aquatic life. There is, however, an abundance of evidence that HABs and these climate change stressors frequently co-occur in coastal zones, which are often considered harbingers of future ocean conditions. For example, many HABs, especially those in freshwater bodies, occur during peak summer temperatures that may already be stressful to aquatic life (Pörtner and Farrell, 2008; Doney et al., 2012). The extreme levels of biomass generated by many ecosystem disruptive HABs (Sunda et al., 2006) can also create high levels of organic matter which, when respired, promotes hypoxia and acidification (Wallace et al., 2014).

While climate change research has typically linked warming, low oxygen, and acidification, it has typically not invoked HABs as an additional stressor to consider. Given the frequent co-occurrence of HABs and climate change co-stressors, and the ability of climate change to intensity HABs, it seems appropriate that HABs be considered a climate change co-stressor. Climate change may act to make HABs become more frequent and intense in some, but not all, coastal ecosystems (IPCC, 2019; Ho et al., 2019). Regardless of how the intensity of HABs change, the certainty of ecosystems becoming warmer, lower in oxygen, and more acidified while HABs and/or their toxins are present creates a scenario that is a more serious physiological threat to aquatic life than the climate change stressors alone. Surprisingly, there is an extreme scarcity of data to understand the nature of this threat, despite the certitude that the co-occurrence of HABs and climate change stressors will become more common in the future.

While there is a wealth of uncertainty regarding HABs and climate change, there is one key certainty: Future HABs will occur in an anthropogenically-altered ocean and, therefore, future occurrence and impacts will differ from what we know today. It is in consideration of all these topics that this Special Issue of Harmful Algae, *Climate change and harmful algal blooms: Insights and Perspective*, was compiled. The Special Issue consists of a dozen articles that consider how specific types of HABs (benthic, pelagic, freshwater, cyst-forming) may respond to climate change as well as how specific climate change processes (acidification) and other concurrent processes (eutrophication) may alter the dynamics of HABs. The Special Issue considers approaches that will be important for studying the effects of climate change on HABs (molecular tools, modeling) and how climate change may act and interact to change the effects of HABs on food webs (aquaculture, fisheries).

Several papers of this special issue focus on major groups of HABs. For example, Trainer et al. (2020) focus on climate change effects on pelagic HABs and do so by specifically focusing on three of the largest and most significant HAB events this century: the new occurrence and spread of *Alexandrium catenella* blooms across south-eastern Australia, the 2015 *Pseudo-nitzschia* bloom that spanned more than 30 degrees of latitude from Alaska to Mexico, and the 2016 "Godzilla red tide" of *A. catenella* and *Pseudochattonella verruculosa* in Chile that caused nearly $1B USD in fisheries losses. The authors specifically explore the role of temperature trends and anomalies as well as coupled ocean-atmospheric forcing in the occurrence of each of these events. Tester et al. (2020) explore how changing climate will alter and impact the occurrence of benthic HABs formed by dinoflagellates in the genus *Gambierdiscus* and *Ostreopsis*, and specifically outline how temperature changes may permit an intensification of these events within some regions as well as a spread of these events pole-ward and into deeper waters.

Freshwater HABs caused by toxic cyanobacteria (cyanoHABs) provide some of the clearest examples of HABs promoted by climate change and anthropogenic forcing (Paerl and Huisman, 2008, 2009). Beyond intensifying HABs, in this issue, Olofsson et al. (2020) demonstrate how four decades of climate change processes has differentially altered the relative abundance of different cyanoHAB genera in the Baltic Sea. Burford et al. (2020) emphasize the many knowledge gaps that exist regarding cyanoHABs and climate change, highlighting the frequent mis-match between the individual studies of cyanoHABs and complexity and time-scale of climate change processes. Beyond providing a comprehensive review of the science of climate change and cyanoHABs, Burford et al. (2020) also highlight future research needed to facilitate better prediction and management of future cyanoHABs.

A final group of HABs considered in this special issue are those caused by cyst-forming dinoflagellates with an emphasis on *A. catenella*. Dormancy and excystment of dinoflagellate cysts is strongly controlled by temperature (Fischer et al., 2018). In this issue, Brosnahan et al. (2020) consider how current and future annual cycles in temperature

may influence the dynamics of dinoflagellate HABs and demonstrate how, as warming moves the favorable habitats for *A. catenella* poleward, it may also allow shallow, inshore habitats to retain resting cysts longer than deep offshore ones, promoting HAB impacts that are more localized and commence earlier each year in these regions.

As emphasized earlier in this preface, one of the great complexities of climate change is the vast number of processes that are changing concurrently. One of these processes is eutrophication. While anthropogenic changes to nutrient loads can intensify HABs (Heisler et al., 2008), climate change processes such as altered patterns of precipitation can independently intensify nutrient loading rates (Sinha et al., 2017) and, in turn, affect HABs. Glibert (2020) examines how climate change in unison with changes to coastal nutrient loading, stoichiometry, and forms might alter the occurrence of HABs. The manuscript demonstrates that concurrent climate and nutrient changes are likely to favor mixotrophic algae over diatoms and concludes that, absent a control on nitrogen loading, more HABs will occur in future oceans. Raven et al. (2020) focus on how rising CO_2 levels might be expected to impact HABs. The paper highlights the interaction between atmospheric and local forcing of CO_2 that can result in systems being acidified, basified, or both over an annual cycle or even over a day-night cycle. The paper also demonstrates that although many HABs appear to grow more rapidly under high CO_2 conditions, the precise response of individual HABs to such conditions can vary at the species and even strain level. Beyond the effects of changes in CO_2 on HAB photosynthesis, the paper highlights how altered pH can alter algal physiology and highlights future directions for research on this topic.

One of the most common themes of the manuscripts presented within this Special Issue is the need for more studies to better understand how climate change will affect HABs. Wells et al. (2020) present findings from a symposium on HABs and climate change and emphasize and review approaches useful for deepening our understanding of HAB-climate change interactions. They specifically highlight the relative utility of laboratory and field studies, long-term observational programs, retrospective studies, as well as linkages with aquaculture and fisheries to understand the socioeconomic effects of HABs and climate change. The authors also specifically recommend collaborative, standardized studies of a small sub-set of HABs to accelerate community understanding of how they may respond to future climate change. Hennon and Dyhrman (2020) highlight the utility of genomics, transcriptomics, proteomics and metabolomics as tools to provide new insight into HABs experiencing climate change. The authors highlight how 'omics data sets may be used to predict the responses of HABs to climate change and provide examples of how 'omics datasets can be incorporated into predictive numerical models to improve such predictions.

A final approach used to understand HAB responses to climate change is described by Ralston and Moore (2020) who explore the utility of models. The authors compare the relative strengths and weaknesses of statistical and process-based models and emphasize approaches needed to improve the modeling of HAB responses to climate change including the use of ensemble approaches, scenario planning, and down-scaling of global climate models to coastal zones where HABs commonly occur. Finally, the authors evaluate HAB models with long-term observations and make suggestions for how the research community might move forward in developing more robust models to project climate change impacts on HABs and to assess long-term trends associated with climate change.

Lastly, Griffith and Gobler (2020) explore how warming, acidification, deoxygenation, and HABs may act and interact to impact aquatic organisms, both today and in the future. The paper demonstrates that while studies of the effects of HABs or individual climate change stressors on aquatic life have been relatively common, studies assessing their combined impacts have been exceedingly rare ($n \sim 10$). Those doing so have often reported strong species- and strain-specific interactions between HABs and climate change co-stressors, yielding outcomes for aquatic organisms that could not have been predicted based on investigations of these factors individually. The paper provides an ecological and physiological framework for considering HABs as a climate change co-stressor and considers the consequences of their combined occurrence for coastal animals.

This Special Issue on Harmful Algal Blooms and Climate Change is, of course, not the first nor final word on this topic. The collection of papers presented here do summarize the current state of knowledge on this subject and, more importantly, provide direction for future approaches to better understand how climate change will affect HABs and, in turn, effect coastal communities. The substantial effects of climate-driven changes on coastal ecosystems, including the intensification of HABs, are becoming increasing clear. Advances in the understanding and prediction of HABs in a changing world will be needed to formulate plans that minimize their impacts on coastal ecosystems, animals, and human communities.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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