Comprehensive Insights into Harmful Algal Blooms: A Review of Chemical, Physical, Biological, and Climatological Influencers with Predictive Modeling Approaches

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Abstract: Phytoplankton plays an essential role in the biogeochemical cycle because it is at the top of the food chain and is a source of oxygen. Eutrophication causes coastal areas to deteriorate as industrialization accelerates, leading to harmful algal blooms (HABs), severely affecting human and ecological health. The frequency and extent of HAB events potentially may increase due to climate change. HAB outbreaks have led to substantial losses for major coastal economies globally, and therefore have emerged as a critical research focus in environmental sciences. However, the lack of an overview of diverse factors influencing HABs complicates the cause identification and the effective countermeasure development for HAB occurrence, thereby impeding the formulation of targeted strategies for prediction and mitigation. Therefore, this review summarizes the influential factors affecting HABs in coastal areas, including water quality factors (nutrients, salinity, stratification, and biological factors) and climatological factors (temperature, pH and pCO_2, and irradiance and light). Recent work with several harmful algae species suggested that warmer temperatures combined with nutrient variation, stronger stratification, and ocean acidification may increase the growth of some toxic dinoflagellate species. Although the effects of factors vary for different species and locations, the intensification of anthropogenic activities and climate change likely will increase the frequency, outbreak scale, and severity of most coastal HABs. Because predicting HABs is crucial for understanding the factors and synergy affecting their growth and minimizing losses for decision makers and stakeholders, we reviewed models for predicting HABs, including process-based models, traditional statistical-empirical models, and data-driven machine learning models. Predicting HABs becomes more challenging as the spatial distribution of harmful algae is influenced by future climate patterns. This review paper presents a comprehensive overview of the various factors impacting HABs in coastal areas, serving as a valuable resource for decision makers and researchers to design targeted research and mitigation strategies. **DOI: 10.1061/JOEEDU.EEENG-7549.** *© 2024 American Society of Civil Engineers.*

Author keywords: Harmful algal blooms (HABs); Water quality factors; Climatological factors; HAB prediction.

Introduction

Excess nitrogen and phosphorus from both point-source pollution, such as industrial and municipal wastewater discharges, and nonpoint-source pollution, including agricultural practices and urban runoff, can lead to eutrophication and subsequently harmful algal blooms (HABs) in surface water (Glibert 2020). HABs can cause significant ecological and economic consequences, affecting aquatic ecosystems, human health, and industries relying on water resources. Because HABs can release toxins into the environment and cause hypoxia, exposure to coastal water bodies containing HABs can harm human health and endanger marine life, leading to adverse impacts on the tourism and entertainment industries (Neves et al. 2021). Climate change impacts HABs by altering marine physical environmental factors, including changes in nutrient availability, salinity, and precipitation patterns, consequently influencing the frequency, magnitude, biogeography, and toxicity of HABs (Ralston and Moore 2020). In addition, changes in precipitation patterns, extreme weather events, temperatures, and stratification may intensify nutrient loading and HABs (Wells et al. 2020). Therefore, a comprehensive understanding of various factors, such as chemical components, climate change, and other environmental influences, is essential for formulating successful HAB mitigation strategies.

HABs are widespread phenomena worldwide, and the highest numbers of HAB events reported across prosperous coastal areas in Europe, East and Southeast Asia, North America, and the South Pacific regions [Fig. 1(a)]. These regions are characterized by thriving economies, vibrant coastal cities, dense populations, and substantial tourism and fisheries. The intense anthropogenic activities in these regions are potentially linked to the proliferation of HAB events. The pronounced increase in HAB events could challenge the economic stability and well-being of these densely populated areas by disrupting the delicate equilibrium of their local ecosystems. Fig. 1(b) indicates a substantial increase in the frequency of HAB events over time. The peak of HAB events was reached

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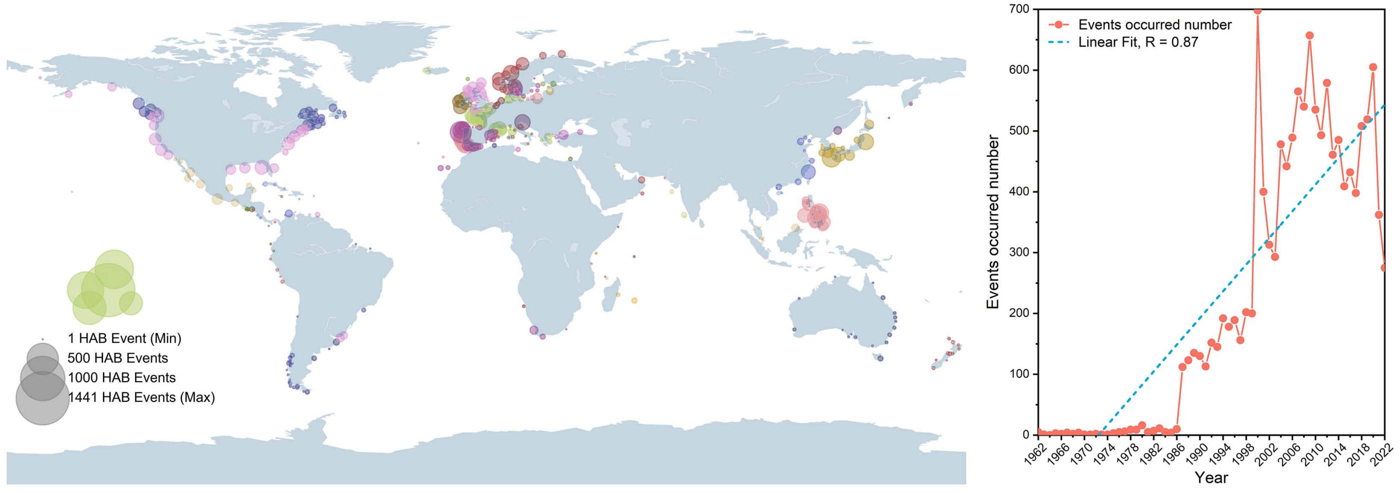

(a)

(b)

Fig. 1. Global HAB events visualization: (a) global HAB visualization in spatial perspective [data from IOC, ICES, and PICES (2021); base map generated using Basemap toolkit version: 1.2.1]; and (b) global HAB visualization in temporal perspective. (The number of HAB events is limited to data accessibility and monitoring conditions).

in 2009, with a remarkable 657 incidents, followed by a decrease in subsequent years; however, the number remained relatively high, 400–600 events annually. An increase in HAB events also was observed in 2020, with 605 events, followed by slight declines in 2021 and 2022. The quantification of HAB events is limited by data accessibility and monitoring conditions. As HAB occurrences continue to rise in various regions, continuous monitoring and research is critical to develop effective management and mitigation strategies. However, there is a noticeable gap in the existing literature assessing influential factors for effectively addressing HABs.

Approach

This study presents a comprehensive literature review from peer-reviewed journals, conference proceedings, case studies, and project reports. We employed wide-ranging keywords and systematically searched hundreds of related publications across reputable sources such as the Web of Science, Wiley, Elsevier, PubMed, Google Scholar, and Springer. The review process included articles published through October 2023. Despite lacking a definitive and consistent explanation for HAB formation mechanisms, this paper provides a thorough exploration of relevant studies, particularly delving into the factors impacting coastal HABs in addition to presenting the models for predicting HAB. We believe this work will be a valuable resource for researchers, policy makers, and environmental experts seeking insights into practical strategies for predicting and mitigating the detrimental impacts of HABs.

Impacts of Water Properties on HABs

Chemical Factors

Phosphorus

Phosphorus is a vital macronutrient for cell metabolism and reproduction processes in all living cells, including algae. In marine environments, phosphorus is available in two forms, dissolved inorganic phosphorus (DIP) and dissolved organic phosphorus (DOP). With increased nitrogen inputs, DIP, which can be used directly by algae species, has become a limiting nutrient in many coastal areas (Wang et al. 2021b). For example, changes in nutrient ratios have led to shifts in phytoplankton populations, such as the transition from diatom to dinoflagellate dominance (Xin et al. 2019). Although phosphorus is essential, HABs still can occur in phosphate-depleted areas (Wang et al. 2021b). Although many algae species directly utilize DIP, some harmful algal species can use DOP as an alternative source by phosphatase enzymes when DIP is scarce, giving them a competitive advantage in HAB formation (Schoffelen et al. 2018). Although there has been some research on the role of phosphorus in HABs, previous studies have focused primarily on DIP, and less emphasis has been given to the complex role of DOP in HAB dynamics. For example, by combining a multiomics approach with stable isotope tracing, future studies may uncover the mechanisms underlying marine dinoflagellate utilization of DOP and their role in bloom formation (Wang et al. 2021a). Furthermore, the interaction between the various forms of phosphorus and specific algal species still needs further investigation, which may provide valuable insights into the intricate relationships between different phosphorus forms and the dynamics of specific algae, contributing to a more comprehensive understanding of HAB life cycle.

Phosphorus availability is a significant factor in influencing HABs in coastal areas subject to high nutrient fluctuations. Coastal regions, particularly in East Asia and the East Mediterranean, often experience P limitation as the main factor restricting HAB formation (Ben Ezra et al. 2021). It is essential to consider seasonal nutrient level changes, because these variations can alter nutrient limitations for harmful algal growth (Schoffelen et al. 2018). However, the current literature has not adequately addressed the impact of the seasonality of phosphorus on HAB formation. Additionally, although higher phosphorus levels tend to support a greater abundance of harmful algae, the complex interactions between various factors contribute to HAB formation. For example, imbalances in N:P ratios caused by human activities may favor toxic dinoflagellates, which can use a broader range of phosphorus sources and adapt to high N:P ratios (Maavara et al. 2020; Wang et al. 2021b). To develop effective and targeted HAB management strategies, it is crucial to conduct further research investigating the nuanced relationships between phosphorus availability, nutrient ratios, and the specific dynamics of harmful algae, enabling a more precise understanding of the factors influencing HABs in coastal environments.

Nitrogen

Algal proliferation is due mainly to the combined addition of nitrogen and phosphorus, especially in coastal areas with rapid urbanization and increased human activities (Anderson et al. 2021). Harmful algae can use various nitrogen sources, including nitrate nitrogen, ammonia nitrogen, and urea, to maintain their proliferation. In addition, they can maximize the use of various nitrogen sources by upregulating transporter gene expression under nitrogen constraints (Zhuang et al. 2013). The role of nitrogen in HAB formation is supported by experimental evidence despite a limited understanding of algal growth mechanisms. For example, Medina et al. (2022) stated that N-rich Caloosahatchee River discharges invariably had increased *K. brevis* blooms throughout time to different degrees. Previous modeling studies that included nitrogen in predicting HABs showed the importance of nitrogen in the results (Xia et al. 2020). High nitrogen levels can increase the growth of N-limited species specifically (Table 1).

Although most studies focused only on inorganic nitrogen, organic nitrogen is also a nutritional source for algal proliferation. Some studies indicated that harmful algae species in California and West Florida Shelf could utilize both inorganic and organic nitrogen (Anderson et al. 2021). Urea is a principal source of organic nitrogen for mixotrophic harmful algal species, especially for dinoflagellates (Huang et al. 2020). Mixotrophic harmful algal species can acquire energy through photosynthesis and organic matter (Li et al. 2021a). Although many studies reported an increase in HABs due to higher nitrogen levels, HAB occurrence does not consistently correlate positively with nitrogen level. This is partly due to the complexity of the growth mechanisms and varying nitrogen requirements among algal species (Wurtsbaugh et al. 2019). Thus, there is a need to investigate the nexus of species-specific growth mechanisms and their distinct responses to various nitrogen inputs.

The Ratio of Nutrients

Combined phosphorus and nitrogen enrichment has been reported to stimulate HABs more than P or N alone, emphasizing the importance of understanding the dynamics of both nutrients for effective HAB control (Paerl et al. 2016). In addition, some specific HAB species may be more limited by nitrogen or phosphorus than others (Table 1). Thus, the growth of these species can be impacted greatly by the availability of these nutrients in the water, and an excess or deficiency of either nutrient may result in a bloom or decline of a particular HAB species.

Nutrient ratios play a significant role in regulating bloom formation; the Redfield ratio ($C:N:P = 106:16:1$) is a critical metric that often is used to determine nutrient limitation. Recent studies showed that the N:P ratio had increased in the Northern Adriatic Sea from 64 to more than 100, in the Northern Gulf of Mexico to more than 16, in the East China Sea to more than 100, and in many other coastal areas (Huang et al. 2019; Malone and Newton 2020). These elevated N:P ratios in many coastal waters affected different algal species in various ways. For example, Xiao et al. (2018) claimed that HAB occurrence often was related to the variation of the N:P ratio rather than to the concentration. Overall, based on available studies, an increased N:P ratio is more favorable for the survival of toxic dinoflagellates and worse for diatoms due to higher phosphorus requirements (Table 2). Although other nutrient ratios, such as nitrogen:silicon, P:Si, and iron:phosphorus, also may play a role in HAB development, they have not been investigated as frequently, highlighting the need for further research to better understand their impact on HABs, especially in environmentally relevant concentrations of nutrients.

Trace Nutrients (Trace Metals and Vitamins)

Trace metals, such as iron, manganese, zinc, and selenium, are vital to algae development and metabolism and are crucial for cellular processes, including photosynthesis, protein and chlorophyll synthesis, respiration, and nitrogen assimilation (Lohan and Tagliabue 2018). Tian et al. (2018) found that aerosols transported by the northwest monsoon enriched with phosphorus, iron, and other trace metals can stimulate HABs in the East China Sea. Selenium is another trace metal necessary for protein synthesis which provides ecological advantages to certain algal species, such as *Aureococcus anophagefferens* (Gobler et al. 2011). The demand for trace metals is influenced by light intensity, nutrient availability, and CO_2 levels (Strzepek et al. 2019). In addition to trace metals, vitamins play a crucial role in the growth and development of algae, acting as cofactors in many enzymatic reactions and participating in the synthesis of metabolites, especially Vitamin B_{12} (Lin et al. 2022). For example, King et al. (2011) claimed that vitamin B_{12}-replete cells had approximately 50% higher specific growth and carbon fixation rates than B_{12}-deficient cells under certain conditions. Although previous studies primarily focused on the role of macronutrients in influencing HABs, trace metals and vitamins often are overlooked in ecological studies, despite their significance in the composition and metabolism of algae community. Additionally, determining the impacts of trace elements poses challenges due to the complexities and variations in natural environmental conditions compared with controlled laboratory situations. These gaps in understanding need to be addressed to gain a comprehensive perspective of the role of micronutrients in algal dynamics and effectively manage and mitigate HABs.

Table 1. Summary of limiting nutrients for growth of some harmful algae species

HAB species or indicator	Limiting nutrient	Research location	Reference
Frequency of red tide	P-limited	Jiulong River Estuary	Wu et al. (2017)
Chlorophyll a concentration	P-limited	East China Sea	Huang et al. (2019)
Gymnodinium impudicum	P-limited	South Sea of Korea	Oh et al. (2010)
Karlodinium veneficum	P-limited	Delaware Inland Bays	Fu et al. (2010)
Prorocentrum minimum	N-limited	Chesapeake Bay	Li et al. (2011)
Prorocentrum shikokuense	P-limited	Between Dongtou and Nanji Islands	Shen et al. (2023)
Alexandrium monilatum	N-limited (summer and fall) and P-limited (winter and spring)	Chesapeake Bay	Killberg-Thoreson et al. (2021)
Karenia brevis	N-limited	Charlotte Harbor estuary	Medina et al. (2022)
Cochlodinium polykrikoides	N-limited	New York estuaries	Gobler et al. (2012)
Phytoplankton biomass and composition	N-limited	Kenya's coastal and marine waters	Oduor et al. (2023)

Table 2. Summary of effect of N:P ratio on growth of some harmful algae species

Location	N:P ratio (atomic)	Dominant harmful algae	Reference
Neuse Estuary	16–18	*Prorocentrum minimum*	Springer et al. (2005)
Chesapeake Bay	<16	*Prorocentrum minimum*	Li et al. (2015)
Zhanjiang Bay	>16	*Skeletonema costatum* and *Phaeocystis globosa*	Zhang et al. (2022)
East China Sea	DIN:DIP < 20	*Karenia mikimotoi*	Li et al. (2009)
	DIN:DIP > 40	Diatoms	
Tolo Harbour	6–15	Non-siliceous phytoplankton	Hodgkiss and Ho (1997)
Southwest Florida Shelf	<8	Dinoflagellates	Heil et al. (2007)
	>24	Diatoms	
Ago Bay, Imari Bay, and so forth	12.3 (optimal)	*Heterocapsa circularisquama*	Yamaguchi et al. (2001)
Kure Bay	16	*Alexandrium tamarense*	Murata et al. (2012)
Ancona, North Adriatic Sea	~24	*Ostreopsis cf. ovata*	Accoroni et al. (2015)
Patagonian fjords	<16	*Heterosigma akashiwo*	Mardones et al. (2023)
Bohai Sea	>16	Dinoflagellates	Yang et al. (2023)
Global research weight average	14.9	Diatoms	Hillebrand et al. (2013)
	15.1	Dinoflagellates	

Silicon

Dissolved silicates (DSi) are indispensable for the growth of diatoms. Silica is considered to be one of the primary limiting nutrients for diatom growth (Lü et al. 2020). For example, an increase in certain diatom species, such as *Pseudo-nitzschia fraudulenta*, has been correlated with high Si concentrations (Tatters et al. 2012). The availability of DSi also impacts the migration patterns of different algal taxa, further influencing ecological dynamics (Zhou et al. 2017). Although the intensification of human activities has led to an increase in N and P supply to coastal marine ecosystems, the DSi content remains stable or decreases due to increasing upstream interception (Maavara et al. 2020). As a result, many studies have proposed that an increase in N:Si and P:Si ratios promotes dinoflagellate growth over that of diatoms (Lü et al. 2020; Ren et al. 2020). This change in nutrient ratios is expected to lead to more frequent and more severe HABs, particularly in the downstream estuaries of rapidly developing regions (Zhou et al. 2017). A shift in the proportion of diatoms in the phytoplankton community can have adverse ecological consequences, affecting the entire food web from phytoplankton to zooplankton and higher trophic levels (Lü et al. 2020). Maavara et al. (2020) predicted that increased dam construction will lead to decreased ratios of RSi:TN and RSi:RP in coastal areas by 2050, with silicon limitation occurring mainly in Southeast Asia, South America, and Africa. This decreasing trend of DSi near estuaries may intensify the effect of DSi on HABs, causing dinoflagellates gradually to replace diatoms as dominant species in some progressively thriving coastal areas. Research on silicon limitation is relatively scarce compared with that on nitrogen and phosphorus, but silicon contributes significantly to determining dominant species in some coastal areas. In cases in which diatoms exhibit toxicity, controlling silicon proves to be a viable strategy. However, when diatoms are nontoxic in the environment and dinoflagellates become dominant and toxic, the removal of silicon elements should not be pursued. To prevent the extensive occurrence of HABs in future scenarios, silicon, which is an essential element for diatoms, plays a crucial role in HAB management and mitigation in coastal ecosystems.

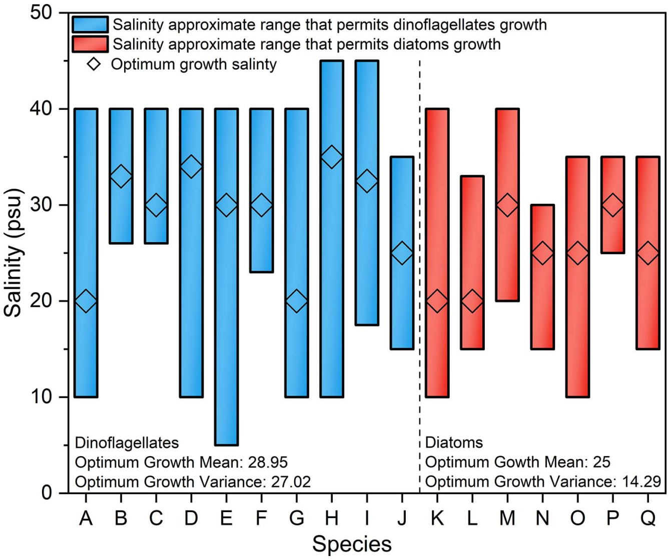

Fig. 2. Summary of the suitable and optimal salinity for the growth of some harmful algae species: (a) *Akashiwo sanguinea* (Matsubara et al. 2007); (b) *Amphidnium klebsii* (Morton et al. 1992); (c) *Gambierdiscus toxicus* (Morton et al. 1992); (d) *Cochlodinium polykrikoides* (Kim et al. 2004); (e) *Gyrodinium instriatum* (Nagasoe et al. 2006); (f) *Prorocentrum lima* (Morton et al. 1992); (g) *Paragymnodinium shiwhaense* (Jeong et al. 2018); (h) *Pyrodinium bahamense* (Usup et al. 2012); (i) *Karenia brevis* (Maier Brown et al. 2006); (j) *Fukuyoa koreansis* (Li et al. 2021c); (k) *Pseudo-nitzschia multiseries* (Doucette et al. 2008); (l) *Asteroplanus karianus* (Shikata et al. 2015); (m) *Pseudo-nitzschia seriata* (Weber et al. 2021); (n) *Pseudo-nitzschia pungens* (Pednekar et al. 2018); (o) *Coscinodiscus wailesii* (Nishikawa and Yamaguchi 2008); (p) *Pseudo-nitzschia circumpora* (Lim et al. 2012); and (q) *Skeletonema costatum* (McQuoid 2005).

Physical Factors

Salinity

Algae growth is critically limited by salinity, because salinity impacts the physiology, metabolism, and distribution of algal species. Toxic dinoflagellates may have higher salt tolerance than diatoms (Fig. 2), because their average optimal salinity is slightly higher, and diatoms prefer relatively lower salinity (Zhou et al. 2019). The response of various phytoplankton species to salinity fluctuations is diverse. Whereas some species, such as *Pyrodinium bahamense*, *Gyrodinium instriatum*, and *Karenia brevis*, exhibited lower growth rates as salinity decreased, other species, such as *Prymnesium parvum*, demonstrated higher growth rates at low salinity (Maier Brown et al. 2006; Nagasoe et al. 2006; Rashel 2020;

Usup et al. 2012). Under the pressure of severe climate change and incremental human activities, the salinity of marine coastal areas and estuaries may fluctuate wildly (Jeong et al. 2018). However, toxic dinoflagellates and diatoms exhibit significant broad tolerance ranges for salinity (Fig. 2), making it challenging to determine the competitive advantageous taxa in future scenarios. In terms of salinity variance, both groups contain euryhaline species capable of thriving in fluctuating estuarine conditions, such as *Pseudo-nitzschia* and *Karlodinium* (Pednekar et al. 2018; Li et al. 2022a). Nutrients, temperature, light, and grazing are crucial factors determining bloom formation and dominance, and salinity alone does not solely dictate competitive advantage. Complex and altering coastal salinity patterns combined with climate change and human activities may allow harmful algal species to expand into new areas and shift competitive dynamics between diatoms, dinoflagellates, and other toxic groups (Wells et al. 2015). More research is required to understand the salinity tolerances of different HAB species and how salinity variability will affect future HAB events in coastal ecosystems.

Stratification

Stratification has a significant impact on the nutrient availability and distribution of oceanic phytoplankton, and thus can contribute to the formation and persistence of HABs. Stratification or vertical density gradients, caused by salinity, temperature, and mixing processes, can favor the survival and proliferation of some phytoplankton species (Griffith and Gobler 2020). Stratification intensifies the pycnocline, forming a thin subsurface layer that acts as a focal point for algal blooms, accounting for 50%–75% of total biomass in the water column and impacting various biological processes, including proliferation and toxin production (Wells et al. 2015). Large-scale climate anomalies can lead to events such as the largest recorded fish mortality, which was caused by a thin layer of *Pseudochattonella verruculosa* in Reloncaví Sound (Mardones et al. 2021). Although diatoms generally are considered to be adversely affected by increasing stratification, they also commonly are found in these thin layers. For example, McManus et al. (2021) found that *Pseudo-nitzschia* spp. was the most abundant phytoplankton in the thin layer in Monterey Bay. Studies have shown that there is a close relationship between water column stratification and an increase in cell abundance of HAB species such as dinoflagellate *Karlodinium veneficum* and *Penicillium verruculosa* (Dai et al. 2014; Mardones et al. 2021). Furthermore, stratification is projected to intensify, especially in middle and high latitudes, due to shifts in global environmental conditions such as increasing temperature and precipitation, and runoff. This change benefits thermophilic, swimming harmful algae such as dinoflagellates over other species due to their ability to move across layers to access nutrients (Wells et al. 2015). Although there is no established causal mechanism linking stratification and HABs, understanding thin layers' dynamics is essential for managing HABs due to the potential increased frequency and intensity of stratification under climate change. Testing the hypothesis linking intensified stratification with increased future coastal HABs will be challenging, because the driving factors of HAB occurrences are poorly understood. It might be possible to identify current and future HAB trends through more-comprehensive experimental data, including stratification intensity and HAB occurrences, along with correlation and causal analyses, shedding light on this complex interplay.

Impacts of Biological Factors on HABs

Algal bloom formation is influenced by a combination of biological factors, including competition, grazing pressure, and adaptability among organisms. In all coastal environments, various phytoplankton taxa vie for essential resources such as nutrients and light, creating a competitive landscape that influences the occurrence and persistence of HABs. As primary producers in the food chain, phytoplankton capture solar energy and inorganic compounds through a photosystem (Shen et al. 2023). Some phytoplankton, such as dinoflagellates, can convert solar energy directly into adenosine triphosphate (ATP), thus gaining a competitive ecological advantage and forming blooms (Zhang et al. 2019). In addition, phagotrophic dinoflagellates are mixotrophs, and have a mechanism to use alternative pathways to obtain carbon (Flynn et al. 2018). For example, *Alexandrium pohangense* and *Karlodinium veneficum* can consume other algae to obtain energy, carbon, and other organics in environments in which light sources are insufficient (Li et al. 2022a; Lim et al. 2019). Vertical migration helps motile species such as dinoflagellates and raphidophytes gather nutrients by moving to the water surface during the photoperiod and sinking during darkness (Lin et al. 2019). Furthermore, allelopathic interactions, in which specific algal taxa release bioactive compounds that inhibit co-occurring species, increasingly are recognized as drivers of HAB formation and sustenance in all coastal environments (Yang et al. 2019). *Karlodinium veneficum* and *Alexandrium* species produce allelochemicals that suppress the growth of competing phytoplankton and microzooplankton grazers (Shang et al. 2021; Yang et al. 2019). Allelopathy is a mechanism that gives toxic HAB-formers competitive dominance under growth-limited conditions. By suppressing co-occurring algal species and reducing grazing pressure via allelopathy, toxic HAB genera can increase rapidly and form extensive monospecific blooms.

Grazing pressure from predators or grazers, such as microzooplankton, mesozooplankton, benthic invertebrates, and fish, from small to large in scale, play a significant role in influencing phytoplankton biomass (Wells et al. 2015). Microzooplankton, mostly less than 200 μm, including heterotrophic dinoflagellates and ciliates, are critical grazers, preying on approximately 65% of harmful algae (Turner 2006). Among benthic invertebrate grazers, shellfish are notable predators of harmful algae and carriers of shellfish poisoning that can damage human health. Dinoflagellates may evade zooplankton predation while accessing nutrient-rich lower water levels, providing a competitive advantage (Wells et al. 2015). Although grazers can affect HAB formation and ecological experiments have tested a few hypotheses, such as bloom forms when the population expansion outpaces the grazing rate, it still is challenging to fully understand the relationship between grazers and HABs. The complexity of these interactions necessitates the establishment of relevant predator–prey ecological models through more-extensive field monitoring and simulation investigations.

The unique biological adaptability of harmful algae to diverse environmental conditions is pivotal in their ecological success and the potential for forming HABs (Karlson et al. 2021). Because brackish and marine coastal environments generally exhibit distinct physical and biochemical characteristics due to salinity differences, these environmental disparities significantly influence the conditions for harmful algae growth. For example, in brackish zones such as estuaries, HAB events often favor euryhaline species due to extensive salinity variations from episodic freshwater inputs. Taxa such as *Pseudo-nitzschia* display physiological adaptations enabling growth across steep salinity gradients in these tidally influenced mixing zones (Ayache et al. 2019). In contrast, marine coastal HABs experience low-scale salinity fluctuations, primarily from precipitation, stratification, and upwelling. However, dinoflagellate species exhibit vertical migratory behaviors to locate optimal salinity niches throughout the water column, fitting well in all coastal areas (Zheng et al. 2023). The differences in salinity regimes between dynamic brackish and more-stable marine coastal habitats select HAB taxa with distinct salinity tolerances.

The biological adaptability of harmful algae to various environmental conditions, such as nutrient levels and light availability, significantly influences their capacity to form HABs. Brackish waters exhibit considerable nutrient variations from terrestrial runoff, leading to intermittent high N and P influxes that fuel HABs (Raven et al. 2020). *Skeletonema* display rapid uptake kinetics to capitalize on nutrient loading in estuaries (Huang et al. 2020). In contrast, nutrients of marine coastal harmful algae, such as *Karenia brevis*, derive primarily from upwelling, aerial deposition, and slower advection and current (Weisberg et al. 2016). IN terms of light availability, turbid brackish zones inhibit light penetration, favoring mixotrophic algae, such as *Karlodinium veneficum*, which supplement phototrophy with phagotrophy (Li et al. 2022a). Differing optical conditions favor flexible utilization of multiple nutritional modes in brackish systems over more-specialized photophysiology in marine coastal environments. In conclusion, mixotrophic harmful algae that can migrate vertically and withstand salinity variability with rapid uptake kinetics have advantages in the more dynamic brackish zones over taxa adapted to relatively stable marine coastal habitats.

Impacts of Climatological Factors on HABs

Temperature

Temperature is a key climatic factor influencing physiological processes in phytoplankton, such as metabolism, germination, nutrient uptake, photosynthesis, and movement (Wells et al. 2015). The increase in sea surface temperature (SST) will not be uniform globally, and coastal areas are predicted to undergo more-significant changes, particularly in high-latitude areas (Robson et al. 2016). As SST becomes warmer, the spatiotemporal growth window of most algae is expected to expand, such as through a shift or extension in the growth period by starting earlier or ending later, along with changes in distribution (Glibert 2020). For example, Jacobs et al. (2015) calculated shifts in the timing of temperature growth windows for *Alexandrium* in Puget Sound and Chesapeake Bay, and found that the bloom period is projected to begin 1 month earlier and end 1 month later. Increased temperatures also may impede the vertical mixing of water bodies, granting a competitive advantage to algae with migratory behavior, such as dinoflagellates. Numerous studies have provided evidence to support the link between increasing SST and a higher likelihood of HAB events (Xia et al. 2020; Xiao et al. 2018). For example, Zhou et al. (2021) found a significant positive correlation between abnormal SST and the occurrence of HABs in the East China Sea over 32 years. Some regions experience large-scale *Pseudo-nitzschia* blooms on the west coast of the US due to a combination of regional SST rises and seasonal upwelling events (Trainer et al. 2020). Machine learning algorithms applied to predict algae blooms showed that temperature was the most crucial driver of bloom formation (Valbi et al. 2019).

Overall, the impact of temperature on HABs varies depending on the specific species of algae involved. For example, toxic dinoflagellates, such as *Alexandrium minutum*, typically have broader temperature growth windows and tend to increase in abundance with rising SST (Thangaraj et al. 2022). Conversely, other species, such as *Karenia selliformis*, are more adapted to colder environments and may be adversely affected by ocean warming (Vellojin et al. 2023). However, toxic dinoflagellates generally may gain a competitive advantage in coastal regions over diatoms, because they often prefer warmer conditions (Fig. 3). Despite the significance of temperature for HABs, there remains a substantial knowledge gap in understanding the mechanisms underlying temperature effects on different algal species, especially in complex coastal environments under uncertain future climate scenarios. Consequently, conducting further experimental and simulation studies is crucial for comprehending the intricate interplay between coastal sea temperature variations and HAB occurrences, thereby providing a comprehensive assessment of temperature's impact on diverse HAB species.

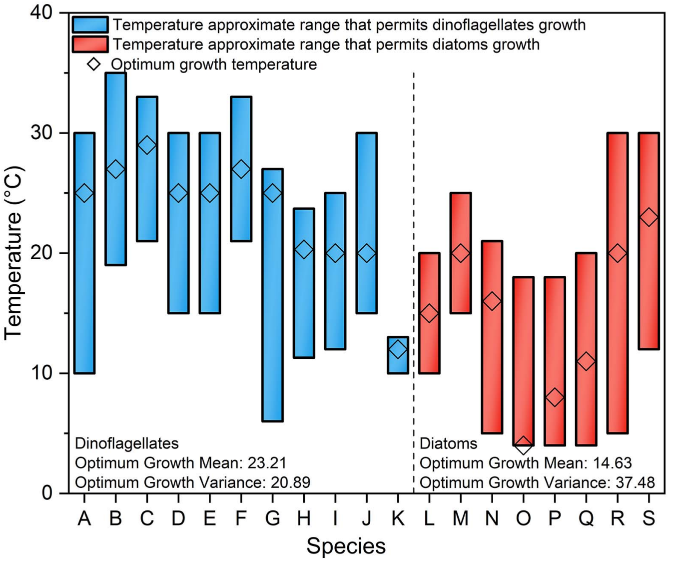

Fig. 3. Summary of the suitable and optimal temperature for the growth of some harmful algae species: (a) *Akashiwo sanguinea* (Matsubara et al. 2007); (b) *Amphidnium klebsii* (Morton et al. 1992); (c) *Gambierdiscus toxicus* (Morton et al. 1992); (d) *Cochlodinium polykrikoides* (Kim et al. 2004); (e) *Gyrodinium instriatum* (Nagasoe et al. 2006); (f) *Prorocentrum lima* (Morton et al. 1992); (g) *Paragymnodinium shiwhaense* (Jeong et al. 2018); (h) *Alexandrium ostenfeldii* (Jensen and Moestrup 1997); (i) *Karlodinium veneficum* (Lin et al. 2018); (j) *Alexandrium pohangense* (Lim et al. 2019); (k) *Karenia selliformis* (Vellojin et al. 2023); (l) *Asteroplanus karianus* (Matsubara et al. 2022); (m) *Asteroplanus karianus* (Shikata et al. 2015); (n) *Pseudo-nitzschia australis* (Thorel et al. 2014); (o) *Chaetoceros convolutes* (Harrison et al. 1993); (p) *Chaetoceros concavicornis* (Harrison et al. 1993); (q) *Thalassiosira allenii* (Aydýn et al. 2009); (r) *Coscinodiscus wailesii* (Nishikawa and Yamaguchi 2008); and (s) *Pseudo-nitzschia australis* (Zhu et al. 2017).

pH and Partial Pressure of Carbon Dioxide

Since the industrial revolution, the widespread use of fossil fuels has increased CO_2 emissions, contributing to ocean acidification. This significantly can impact the physiology of various algae species, resulting in changes in carbon fixation and nutrient absorption rates, increased sensitivity to UV radiation, and alterations in intrinsic element composition (Fu et al. 2012). The impact of increased partial pressure of carbon dioxide (pCO_2), which corresponds to lower pH, on HABs varies across species. Some toxic dinoflagellates may benefit from higher pCO_2 in photosynthetic carbon fixation, because their CO_2 fixation enzymes can reduce the energy demand of the carbon concentrating mechanism. For example, Vellojin et al. (2023) reported that *Karenia selliformis* may benefit from relatively lower pH values, leading the species to bloom during autumn. Li et al. (2022b) reported that *Prorocentrum minimum* concentrations in Chesapeake Bay are predicted to increase by 2.9% by 2050 due to lower pH levels. However, Kremp et al. (2012) found that the increase in CO_2 stimulated only two of the eight *Alexandrium ostenfeldii* clones isolated from the Baltic Sea. Fu et al. (2008) claimed that the increase in pCO_2 would promote the carbon fixation rate of *Prorocentrum minimum* but would not affect its growth rate significantly. Conversely, diatoms' responses to ocean acidification vary. Tatters et al. (2012) and Sun et al. (2011) suggested that ocean acidification and increasing abundant carbon sources might greatly intensify *Pseudo-nitzschia* blooms, whereas other studies stated that the impact of elevated pCO_2 might be negligible or even might reduce biomass (Ayache et al. 2021; Dutkiewicz et al. 2015).

The response of algae to ocean acidification primarily focuses on changes in carbon concentrations rather than pH, because published studies often cannot distinguish between the direct pH and pCO_2 effects (Raven et al. 2020). Overall, the impact of pH on HABs depends on the optimal growth window of specific harmful algae species, and some species thrive in coastal areas due to increased pCO_2 and adaptation to acidic environments. However, the mechanisms of how changes in extracellular pH affect algal growth processes still are poorly understood.

Irradiance and Light

Light availability is a crucial factor affecting the growth and distribution of phytoplankton. Photosynthetic autotrophs rely on light as their primary energy source, and within a specific range of intensity, their photosynthetic efficiency increases (Lin et al. 2019). However, beyond the light saturation point, photosynthesis may be inhibited. Light conditions in the ocean can vary due to stratification and cloud distribution, influencing the growth and competitive success of HABs (Stocker et al. 2014). Some harmful algae can thrive under various light intensities. For example, *Alexandrium catenella* isolated from Mediterranean waters exhibited a positive correlation between biomass and light intensity (Laabir et al. 2011). Moreover, the ability of *Paragymnodinium shiwhaense* to grow within a broad range of light intensities highlights its potential for competitive success in the future ocean environment (Jeong et al. 2018). However, not all HABs can withstand high light levels without experiencing photoinhibition (Wells et al. 2015). For example, *K. brevis* and *Aureococcus anophagefferens* showed relatively lower light saturation points and were better adapted to lower light-intensity levels, indicating a competitive advantage in high-turbidity environments (Gobler and Sunda 2012). Future climate predictions suggest changing cloud cover at low and high latitudes, which could affect light intensity, thereby impacting HABs (Fu et al. 2012). As a result, understanding the varying sensitivities of different harmful algal species to light intensity is essential for predicting and managing their responses to environmental changes. On-site and off-site studies, combined with climate model predictions, provide valuable insights into the potential shifts in HAB composition.

The Synergistic Effects of Various Factors on HABs

The synergistic effects of various factors on the growth of harmful algae involve the combined and interactive impacts of multiple aspects, including chemical, physical, biological, and climatic factors. For example, Fu et al. (2007) found that the growth rate of *Synechococcus* was greatly increased as a result of the synergistic effect of the increase in CO_2 concentration and temperature. Flores-Moya et al.'s (2012) experimental results showed that prolonged temperature rise and pH decrease could significantly boost the growth rate of *Alexandrium*. Elevated water temperature can create favorable conditions for harmful algae to thrive, and when combined with stratification, the growth of some toxic dinoflagellates can be even more rapid (Wells et al. 2020). In addition, Xiao et al. (2018) found that low temperature and high nutrients favor diatom blooms, whereas low phosphorus and high N:P ratio are more conducive to dinoflagellate blooms in the East China Sea. With the intensification of climate change and human activities, almost all important factors affecting HABs will vary dramatically in the future. The growth and dissipation of HABs are not dependent solely on single-variable shifts, as often is controlled in simple laboratory experiments; instead, they result from the synergistic effects of multiple contributing factors. Thus, the impact of individual variables on each other along with their synergistic combined effects need to be investigated to better understand and manage HABs.

HAB Prediction Methods under the Synergistic Effects of Influencing Factors

The accurate prediction and early warning of HAB proliferation in coastal areas have received significant attention due to their potential to mitigate health risks for coastal inhabitants and minimize economic losses in affected regions. Coastal HAB prediction approaches encompass a range of methodologies, including process-based models, traditional statistical-empirical models, and data-driven machine learning (ML) models. Additionally, we discuss whether chlorophyll, which is broadly used as a HAB indicator, can represent harmful algal biomass in HAB predictions.

Process-Based Models

Process-based models are based on the quantitative description of the physical, chemical, and biological processes of HABs (Pinto et al. 2016). Liebig's law of the minimum asserts that the determining factor for growth is not the overall abundance of resources but rather the scarcity of the most limited resource, which is known as the limiting factor (Kim et al. 2022). When one of the essential resources, such as light or nutrients, is inadequate, it restricts the overall growth rate. Liebig's law is vital for representing the algal growth formula in process-based models, providing a theoretical basis for predicting growth kinetics. Liebig's law has been implemented mathematically in HAB models by several approaches, such as the Droop model, Monod model, and multiplicative model. The Droop model represents an algal growth rate as a function of internal cell nutrient status (Droop 1974). Wang et al. (2014) simulated two HAB events and found that the results were compatible with related processes observed in the East China Sea. The Monod model links growth rate to external nutrient concentrations (Monod 1942). However, Monod models may not be the best option for HAB modeling because the nutritional modes of many harmful algae are more complicated than the phototrophic alone, and algae may keep growing even in nutrient-limited situations using their internal stores (Li et al. 2022a). Multiplicative models apply Liebig's law by multiplying limited terms for each essential nutrient and factor (Folt et al. 1999). Jiang et al. (2021) utilized a multiplicative model to predict the interactive effect of suspended particles and nutrients on the growth inhibitory rate of *Amphidinium carterae*. Overall, Liebig's law provides a valuable conceptual framework, but HAB models must move beyond simple single-factor limitations to properly reflect multifaceted growth controls in realistic ecosystems. For mixotrophic algae, this requires additional accounting for both phototrophy and phagotrophy in holistic models coupling light, nutrients, and prey availability to represent the complex synergistic interactions governing growth.

In addition to models grounded in Liebig's law, some process-based models consider a spectrum of influencing factors with intricate biological dynamic processes, constituting HAB events and biomass predictive frameworks. For example, Lin et al. (2018) applied a dynamic mathematical model to simulate the growth of *Karlodinium veneficum* and its prey with further exploration of the impacts of nutrient ratio and temperature on them. Moore et al. (2015) developed a regional three-dimensional (3D) physical model, forced by wind, air temperature, and so forth, to predict *Alexandrium* under the influence of climate change. Process-based models integrating hydrodynamics and biochemical processes consider multiple perspectives from physical, chemical, and biological processes, representing a prominent direction for future HAB modeling. Gillibrand et al. (2016) developed a coupled hydrodynamic–algal transport model to track *Karenia mikimotoi* bloom progression and investigate the influencing factors on *K. mikimotoi* transport and dispersal. Ralston et al. (2015) developed a 3D hydrodynamics-*Alexandrium fundyense* model in Nauset Estuary to investigate recurrent HABs' physical and biological controls, and determined the importance of water temperature for *A. fundyense* blooms. Yñiguez et al. (2018) established a hydrodynamic–*Pyrodinium*–shellfish model to simulate *Pyrodinium* and shellfish toxicity variation, and claimed that precipitation drives bloom seasonality.

Process-based models require precise expressions of HAB life processes, which may be limited due to the lack of understanding of physical–biochemical processes, reference data and parameter quality, and initial and boundary conditions (Flynn and McGillicuddy 2018). Thus, process-based models are inherently complex, making their development time-consuming. Subsequent calibration of these models poses additional challenges. Calibration, which involves model parameter tuning, demands a thorough understanding of the system dynamics, and can be a demanding task to ensure accurate model predictions for each new application. However, they can be applied in different regions and are effective in extrapolating studies under future climate scenarios due to their explicit representation of processes (Ralston and Moore 2020).

Statistical Models

All statistical models establish correlations between environmental variables related to HAB formation and HAB indicators such as HAB biomass, chlorophyll, and toxicity (Flynn and McGillicuddy 2018). Environmental variables typically are selected based on empirical or theoretical knowledge of physical and biochemical processes. These variables then are incorporated into traditional statistical-empirical models for predicting instead of for representing the HAB processes with mathematical equations. Li et al. (2023) used a series of statistical analyses to indicate that the long-term variations in HABs in the Bohai Sea were associated with a combined influence of climate change, eutrophication, and the development of marine aquaculture. Lima et al. (2022) applied empirical-statistical generalized additive models (GAMs) to develop relationships between environmental variables and several HAB species, and found that the most crucial predictors of HAB events are radiation, mixed layer depth, and SST. Zhou et al. (2021) applied a generalized linear model (GLM) framework with a Poisson distribution to determine the primary drivers of HAB events in the East China Sea. Statistical models generally require long-term observational data to establish robust relationships between variables and HAB responses. Although traditional statistical models often have lower prediction accuracy than machine learning models across various fields, they have the advantage of interpretability (Parmezan et al. 2019). For example, GAM model coefficients can be utilized directly to assess the relative importance of features (Ravindra et al. 2019).

Data-Driven Machine Learning Models

Data-driven ML models represent some of the most widely utilized predictive models (Jordan and Mitchell 2015). These models avoid the mathematical expression of physical, chemical, and biological processes that are not yet fully understood. Instead, they use data-driven algorithms to establish black-box models that may have improved predictive capabilities compared with traditional statistical approaches, but they lack interpretability (Parmezan et al. 2019). ML models often are perceived as more straightforward to implement than process-based models, particularly if large data sets are available and the underlying processes are complex or not well-understood. However, the choice between ML and process-based models depends on the specific characteristics of the problem and considerations such as the model interpretability and the availability of sufficient data for training and validation. ML models for predicting HABs usually are divided into the qualitative classification problem of judging whether algal bloom occurs, and the quantitative regression problem of predicting biomass concentrations (Zohdi and Abbaspour 2019). Some recent studies utilizing ML algorithms for predicting HABs are listed in Table 3. By applying emerging ML models, researchers can infer the relationship between environmental conditions and HABs, gaining valuable insights from external metrics such as the Gini index and Shapley additive explanations (SHAP) values (Lundberg and Lee 2017; Yu et al. 2021). However, the relationships inferred are correlative rather than causative. Such methods and models should supplement, not replace, process-based modeling and experimental research to establish causal mechanisms. Insights from interpretable ML should be considered to be hypotheses that should be tested using further ecological knowledge and experiments. One major limitation of ML models is the requirement for extensive historical data and time investment in tuning hyperparameters, thus restricting their applicability when extended to new regions or different HAB species. Moreover, because ML models do not directly incorporate physical processes, but instead learn intrinsic patterns from training data, they may exhibit poorer generalization and robustness, and even pose risks (Schmidt et al. 2018). For example, applying climate change data, such as future temperature projections exceeding all previous temperatures, to the model may yield biased results (Ralston and Moore 2020).

Due to the causal relationships upon which process models are built, they contribute to constraining and guiding ML models. Experimental data provide in-depth insights into HAB dynamics under controlled conditions, and these high-quality data aid in training ML models. ML models excel in utilizing large data sets and uncovering intricate nonlinear relationships that might elude detection in process models or experiments. Therefore, combining different experimental data or process-based models with ML enhances predictive accuracy and addresses extrapolation challenges, such as those encountered in climate change studies. Given the inherent pros and cons of each predictive methodology, future research should prioritize the development of process-based physical–biochemical coupled models, enhancing the representation of complex processes in both HAB onset and decay, collecting and integrating multisource data high-quality data sets, and creating hybrid models that leverage the strengths of all approaches for improved predictions. Strengthening the comprehension and understanding of crucial environmental and biological processes

Table 3. Summary of application of machine learning algorithms to HAB prediction

Predicted species or targets	Features or factors used to predict	Study area	Model used	Best accuracy
Occurrences and cell count of *K. brevis* (Izadi et al. 2021)	Daily ocean color satellite products	Coastal areas of West Florida	XGBoost[a], RF, and SVM	96.2%
Chlorophyll-a concentration (Deng et al. 2021)	TIN, DO, P, turbidity, temperature, BOD5, pH	Tolo Harbour, HK, China	ANN and SVM[a]	$R = 0.98$
Occurrence of *A. minutum* (Valbi et al. 2019)	Day, wind, temperature, pH, salinity, DO, N, P, etc.	NW Adriatic Sea, Italy	RF[a]	85.5%
Pseudo-nitzschia spp. Abundance (Vilas et al. 2014)	Day, temperature, salinity, upwelling indices derived from wind speed	Coastal waters of Galician rias, Spain	SVM[a]	78.57%
K. brevis cell densities (Li et al. 2021b)	Discharge, nutrients, wind, temperature, sea surface height difference	West Florida Shelf	SVM[a], RVM, Naïve Bayes, and ANN	79%
Phytoplankton concentration (Yu et al. 2021)	Ammonia, chlorophyll, NO$_x$, phaeophytin, P, silicate, temperature	Scripps Pier, southern CA, and SishiLi Bay, eastern Shandong, China	GBDT[a], AdaBoost, ANN, KNN, and SVM	$R^2 = 0.969$ (Scripps Pier) $R^2 = 0.617$ (Sishili Bay)
Ostreopsis cf. ovata concentrations (Asnaghi et al. 2017)	Day, temperature, salinity, pressure, wind	Genoa coastline, Italy	Quantile regression forests[a]	$R^2 = 0.43$
Alexandrium catenella cells concentration (Baek et al. 2021)	Salinity, temperature, velocity, retention time, ammonium, P, water surface elevation	Geoje Island, South Korea	DT[a]	75%

Note: Best accuracy refers to the best classification or regression metric received among all models used in the prediction in the reference study. TIN = total inorganic nitrogen; DO = dissolved oxygen; BOD5 = five-day biochemical oxygen demand; XGBoost = extreme gradient boosting; RF = random forest; SVM = support vector machine; ANN = artificial neural network; RVM = relevance vector machine; GBDT = gradient-boosted decision trees; KNN = K-nearest neighbors; and DT = decision tree.

[a] Best-performing algorithm.

influencing HABs and enriching the scientific foundation remain central to advancing the understanding of HABs.

Chlorophyll and Harmful Algal Biomass

Accurate monitoring and prediction of HABs is essential for early warning systems, developing mitigation strategies, and managing fisheries and ecosystems (Zohdi and Abbaspour 2019). However, directly quantifying HAB abundance by counting algal cells is resource-intensive and often limited in geographic scope. Consequently, chlorophyll, which is the primary photosynthetic pigment in algae, has become a widely adopted lower-cost surrogate for estimating algal biomass during blooms (Khan et al. 2021). Widespread use of chlorophyll as an indicator offers prominent advantages over cell counts for monitoring HABs. Quantifying chlorophyll is relatively technically straightforward and inexpensive, especially with the extensive spatial coverage of surface chlorophyll provided by satellite remote sensing, which is valuable for tracking the HAB movement (Izadi et al. 2021). It makes chlorophyll a practical tool for rapidly assessing general HABs over large areas.

Although chlorophyll can be considered to be a useful algal biomass indicator on average, substantial variability exists in the relationship between chlorophyll and biomass across HAB species and growth conditions. Factors such as nutrient availability and light impact chlorophyll production. Nutrient limitation may tend to increase cellular chlorophyll concentration within phytoplankton communities, resulting in an overestimation of biomass when using chlorophyll as an indicator (Browning et al. 2017). Low light exposure also induces chlorophyll synthesis. For example, Jiang et al. (2021) found that *Amphidinium carterae* in turbid environments tends to synthesize more chlorophyll a and to proliferate less, leading to the bias of the chlorophyll–biomass relationship. Cellular chlorophyll content changes over different growth stages. Chlorophyll content tends to increase during the exponential phase and decline or stabilize in the stationary phase (Medić et al. 2022). This temporal variability reduces the reliability of chlorophyll as a proxy. In addition, the relative concentration of chlorophyll within an algal cell varies by species (Basak et al. 2021). Therefore, combined with the aforementioned theories, chlorophyll as an indicator of HABs instead of algal blooms is not sufficiently precise, even though certain harmful algal species may dominate the phytoplankton during specific HAB events. Given the substantial variations in environmental conditions, growth stages, and cell sizes among different algal species, chlorophyll should be considered only an approximate indicator of HAB biomass, at best. Caution is necessary, and limitations must be outlined explicitly when chlorophyll is employed as an indicator for HABs due to challenges in data collection.

Impacts of Influencing Factors on HAB Dissipation and HAB Postprocessing Methods

The dissipation of HABs is influenced intricately by a multitude of factors, ranging from nutrient availability and physicochemical changes to the selective grazing activities of certain organisms. Depletion of limiting nutrients due to active uptake and assimilation during rapid bloom growth can curtail expansion further (Wurtsbaugh et al. 2019). Coastal upwelling or inland runoff may cease to provide new inputs, creating nutrient limitations. The absence of required nutrients reduces growth rates and induces a decline. For example, Xiao et al. (2022) experimented with mineral–hydrogel composites to reduce algal growth by capturing phosphorus. Because most HABs prefer stable environments with higher residence time, physical processes such as wind-driven advection or currents can break up dense surface accumulations, effectively diluting and dispersing the concentrated biomass (Qin and Shen 2019). Many harmful algal species thrive only within specific temperature, salinity, and light ranges. Temperature and salinity changes reduce metabolic rates, and light shifts that move cells away from optimal irradiance levels can inhibit growth. For example, *Karlodinium veneficum* declines sharply with high-temperature treatments (Coyne et al. 2021). An *Alexandrium fundyense* bloom appeared to be suppressed due to early intrusions of lower salinity water into the western Gulf of Maine (Townsend et al. 2014). Physicochemical changes that fall outside the optimal "comfort zone" for these species deter to maintaining conditions conducive to algal blooms. Certain grazers selectively feed on some harmful algal species. Mass grazing may occur if toxin concentrations decrease during the bloom climax, contributing to bloom collapse. A notable example occurred on the French Atlantic coast in 2021, where a massive bloom of toxic *Lingulodinium polyedra* collapsed during the declining phase because *Noctiluca scintillans* extensively grazed on *L. polyedra*, acting as the decisive factor leading to the termination of the bloom (Mertens et al. 2023).

Programmed cell death (PCD) and reproduction with cyst formation are integral processes that contribute to HAB's rapid decline or crash. These phenomena constitute essential components of the natural life cycle in algal species. PCD is a regulatory mechanism that reduces cell numbers in response to unfavorable biotic and abiotic stress conditions (Aguilera et al. 2021). Reproduction in algae, often involving the development of cysts or resting stages, is a vital adaptive strategy, allowing algae to endure adverse environmental conditions and establish a dormant state (Tang et al. 2021). These adaptive mechanisms position the algae to survive and potentially initiate a new bloom when the conditions become conducive. In summary, the eventual dissipation of HABs involves intricate interactions among physical, chemical, and biological factors, with self-regulation ability in unfavorable environmental conditions. Resource managers and stakeholders need a comprehensive understanding of HAB growth and collapse factors for prevention and postprocessing, which is crucial to enhancing predictive models and reducing the extent and severity of harmful impacts.

HABs impose significant ecological, economic, and public health burdens globally with increasing frequency and severity. Depending on the harmful algal species, physical, chemical, and biological methods can be employed to control them following the occurrence of coastal HABs. Physical methods include ultraviolet radiation damaging microalgal cells, ultrasonication affecting algal buoyancy and photosynthesis, and air extraction causing harmful algae to float to the surface for removal (Balaji-Prasath et al. 2022). Most physical methods are costly and challenging for extensive bloom application, and thus primarily are employed as emergency cases rather than preventive strategies (Balaji-Prasath et al. 2022). Chemical methods include engineered nanoparticles causing algal cell damage and higher nutrient consumption and lower photosynthesis rates; algicidal chemicals (such as permanganate, ozone, chlorine, and so forth) for algal cell elimination; and modified clays causing cell flocculation, nutrient removing, and shading (Gallardo-Rodríguez et al. 2019). Chemical methods offer advantages in the efficiency of algal cell damage and elimination; however, they may raise concerns about environmental impact and the potential development of resistant algal strains (Gallardo-Rodríguez et al. 2019). It is crucial to assess the ecological consequences carefully and employ these methods judiciously to mitigate adverse effects on ecosystems. Biological methods include algicidal bacteria, parasitic pathogens, and viruses inhibiting algae growth and causing cell lysis, protistan grazers grazing harmful algae, and allelochemicals from the secondary metabolism of plants and microorganisms to inhibit or kill algae (Pal et al. 2020). Biological methods are considered to be a crucial tool for HAB control, primarily due to their environmentally friendly nature; however, these methods typically require more than 10 days to manifest inhibitory effects (Balaji-Prasath et al. 2022).

Conclusion and Future Directions

This review article summarizes water quality factors (chemical, physical, and biological) and climate factors affecting HABs, and presents an overview of models used for HAB prediction. With the impacts of climate change and anthropogenic activities, the frequency and severity of HABs are gradually increasing. Significant studies should be conducted to identify and analyze the factors affecting HABs. These findings will enable decision makers to specify management plans to protect human and ecological health, the economy, and the environment. Based on the review of research progress, we believe that the following aspects need to be studied:

1. Strengthening the basic research on harmful algae species. Physiology, ecology, and other fundamental processes are essential and theoretical support for research. This review focuses more on the influencing factors of HABs that may be beneficial for prediction. However, if the physiological procedures can be expressed accurately, this will significantly improve our understanding of influencing factors and prediction accuracy.
2. Applying molecular ecology to analyze HABs. The characteristics of organisms are controlled by genes. With the rapid development of high-throughput sequencing technology, sequencing methods should be expanded to detect important gene fragments that control the growth of harmful algae to determine the species' limiting factors directly.
3. Establishing a shared database for single-species influencing factors. Creating a comprehensive, shared database to compile global data on various potential factors influencing harmful algal species would be invaluable for scientists when designing experiments and numerical simulations. Simultaneously, refining data collection methods through adaptive management can strengthen research capabilities further.
4. Simulating environmentally relevant conditions in the experiments. Experimental setups often differ from real-world conditions, because laboratories usually employ control variates to simplify complex problems, potentially overlooking critical factors. Considering environmentally relevant conditions in experimental setups, along with field studies, will be effective in enhancing the understanding of HABs and their complex dynamics.
5. Considering the synergy of influencing factors. The pressure of climate change will change many influencing factors which are critical to the growth of harmful algae. Most influencing factors are related to geographical location, and this complex synergy also will be regulated by spatiotemporal distribution. Therefore, the synergy of multiple factors should be considered when designing experiments or numerical simulations.
6. Combining various prediction methods. Each predictive model has its advantages and disadvantages. Thus, it is recommended that a combination of diverse models, such as physical process-based models, statistical-empirical models, and data-driven machine learning models, should be adopted to predict and explain the changing characteristics of HABs under increasing pressure at present and in the future. Machine learning models have significant potential for HAB prediction but require data sharing

and collaborative research to enhance their generalization and robustness.

7. Attempting to prevent HABs by reducing external nutrient loading into coastal waters, such as from agricultural runoff, wastewater discharge, and wash-off, to decrease the frequency and magnitude of HAB events. For example, catchment-to-coast approaches, such as establishing green infrastructure as buffer zones in urbanized and agricultural coastal areas or allocating resources and prioritizing advanced wastewater treatment processes to reduce nitrogen and phosphorus, can be one of many effective measures.

Data Availability Statement

All data, models, and code generated or used during the study appear in the published article.

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