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Review Article

Stressing over the Complexities of Multiple Stressors in Marine and Estuarine Systems

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Aquatic ecosystems are increasingly threatened by multiple human-induced stressors associated with climate and anthropogenic changes, including warming, nutrient pollution, harmful algal blooms, hypoxia, and changes in CO_2 and pH. These stressors may affect systems additively and synergistically but may also counteract each other. The resultant ecosystem changes occur rapidly, affecting both biotic and abiotic components and their interactions. Moreover, the complexity of interactions increases as one ascends the food web due to differing sensitivities and exposures among life stages and associated species interactions, such as competition and predation. There is also a need to further understand nontraditional food web interactions, such as mixotrophy, which is the ability to combine photosynthesis and feeding by a single organism. The complexity of these interactions and nontraditional food webs presents challenges to ecosystem modeling and management. Developing ecological models to understand multistressor effects is further challenged by the lack of sufficient data on the effects of interactive stressors across different trophic levels and the substantial variability in climate changes on regional scales. To obtain data on a broad suite of interactions, a nested set of experiments can be employed. Modular, coupled, multitrophic level models will provide the flexibility to explore the additive, amplified, propagated, antagonistic, and/or reduced effects that can emerge from the interactions of multiple stressors. Here, the stressors associated with eutrophication and climate change are reviewed, and then example systems from around the world are used to illustrate their complexity and how model scenarios can be used to examine potential future changes.

1. Introduction

Human activities on land are changing aquatic environments in diverse and complex ways with important implications for ecosystems. For many aquatic systems, nutrient pollution leads to eutrophication, temperatures are increasing, carbon dioxide (CO_2) is increasing, and pH is decreasing [1, 2] (Figure 1). These factors have contributed to increasing hypoxia and harmful algal blooms (HABs), which themselves have become stressors and have altered the community of organisms that compete and interact to structure food webs [3] (Figure 2). As a consequence, ecosystem changes are occurring rapidly and in nonlinear ways, and complexity results from the interactions between these mul-

tiple stressors. Classic conceptual relationships regarding stressors and effects (dose-response functions) and future projections based on single-factor responses have limited utility given the multitude of changes occurring now and in the future.

From primary producers and other microbes to upper trophic levels, stressor effects may be direct, but they may also be amplified and propagated, or even subdued and reduced, through food web interactions, biogeochemical alterations, and interactions between stressor effects. Opportunities may emerge for new dominant species as a result of multiple-stressor interactions. The complexity of these interactions creates enormous challenges for biogeochemical and ecosystem modeling and predictions of what may happen in
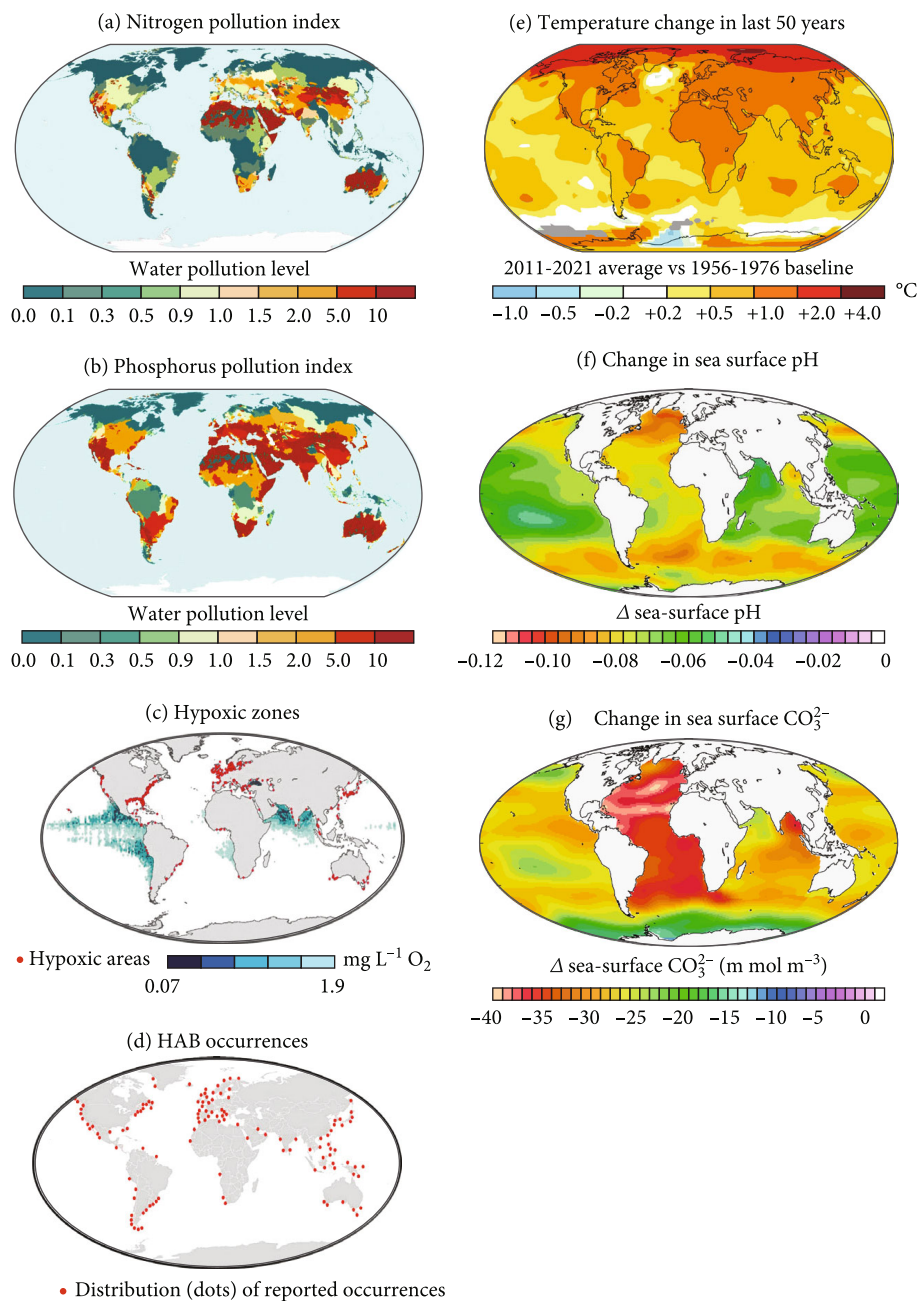
FIGURE 1: Global multiple stressors. Global maps showing (a, b) index of nitrogen and phosphorus pollution per river basin, where values > 1 indicate that the waste assimilation capacity of the river basin is insufficient and nutrient pollution results; (c) hypoxic zones (<2 mg L^{-1} O$_2$, red dots) and oxygen minimum zones at 300 m (blue shaded regions); (d) distribution of reported occurrences of HABs that produce paralytic shellfish poisoning; (e) average air temperature change in the last 50 years (2011-2021 average versus 1956-1976 baseline); (f) estimated change in seawater pH caused by oceanic uptake of anthropogenically created CO$_2$ between the 1700s and the 1990s; (g) estimated change in annual mean sea surface CO$_3^{2-}$ between the 1700s and the 1990s. (a) and (b) are modified from Mekonnen and Hoekstra [8, 9]; (c) is modified from Breitburg et al. [10]; (d) is modified from [11]; (e) is modified from [12]; (f) is modified from [13]; (g) is modified from [14]. All are under Creative Commons licenses.

the future in an even more impacted world; thus, the scenarios of future change encompass large uncertainties. Uncertainties also increase as one ascends the food web. Multiple stressor interactions include direct ecological effects, indirect ecological effects, and those that occur between stressors. Several stressors can be a consequence of other stressors (e.g., HABs can result from nutrient pollution and can lead to hypoxia, and changes in CO$_2$ and pH can result from altered rates of productivity, including from HABs), but they can also be stressors in their own right. While direct ecological effects are straightforward and may follow dose-response characteristics, indirect ecological effects are those that result in responses that are different than those that would occur if considered independently (e.g., warming with
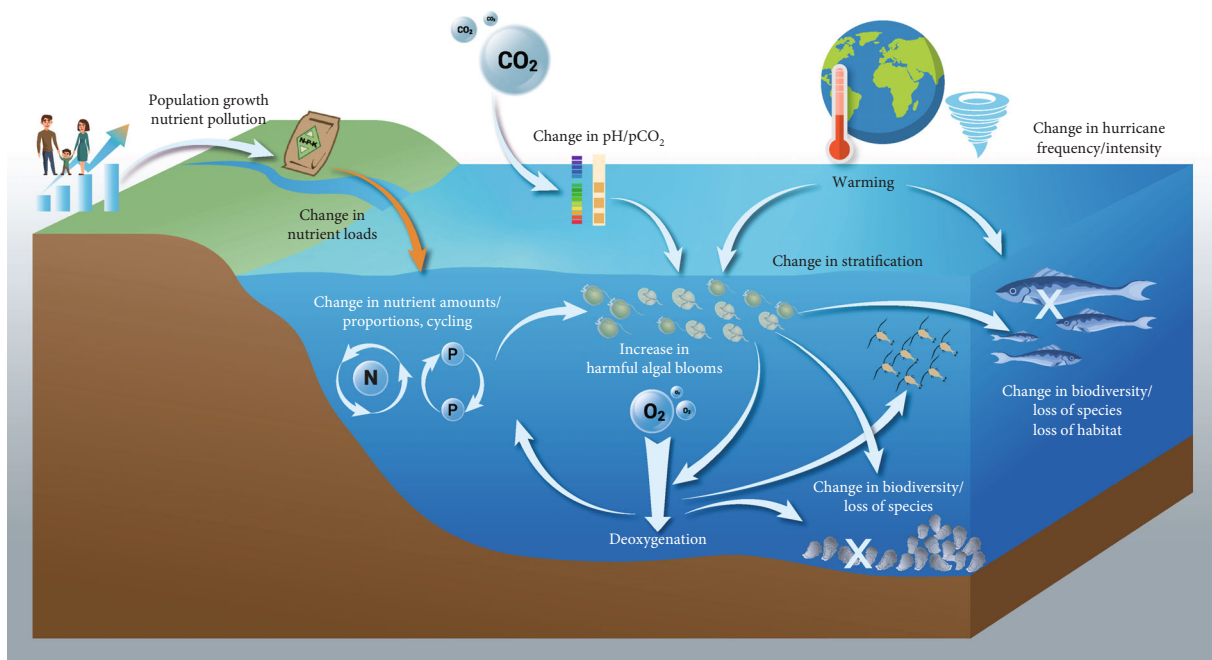
Figure 2: Conceptual diagram of the complexity of interactions of multiple stressors in aquatic systems. Symbols are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science.

deoxygenation causes slower growth of fish than each variable does separately). Interactions between stressors occur when one stressor affects the timing or intensity of another stressor (e.g., warming increases HABs or may change the timing of blooms). Indirect ecological responses and interactions among stressors in higher trophic levels are especially complex because of differing sensitivities and exposures among life stages within a species, and stressors can also alter species interactions such as competition and predation, with cascading effects through the food web. Many protists, including many HAB taxa, are also now recognized to be mixotrophic, in which the dual nutritional modes of autotrophy and heterotrophy are combined in a single organism (e.g., [4]). Many upper trophic level organisms are long-lived and exhibit complex life cycles [5, 6]. The interannual and long-term population dynamics of these upper trophic level organisms are governed by certain life stages (e.g., spawning, larvae, juveniles, and adults) that can vary in importance among years. Many species also have life stages that utilize different habitats that can have different stressor types and levels. There will be winners and losers [7]; for example, a resistant prey species may show a smaller negative response or even a positive response to multiple stressors if their predators are negatively impacted by one or more of the stressors. The complexity of these biological interactions—combined with the complexities of stressor changes—makes modeling and projections of future changes exceedingly challenging.

The goal of this review paper is to highlight areas where our knowledge of biology and biogeochemistry helps us tame some of this complexity and identify how the trajectory of change in different types of aquatic systems can be assessed in coupled model frameworks. Although the list of stressors or potential stressors is extremely long, this paper focuses on nutrient pollution, HABs, hypoxia, warming, and changes in CO_2 and pH, as these stressors are associated with eutrophication and climate change. Several case studies are described to illustrate not only how stressors interact but also how the complexity of stressors may differ between coastal ocean and estuarine ecosystems. A strategy is proposed for how new models that transcend multiple trophic levels may be developed, addressing multiple stressor effects at each level. Such a strategy allows questions to be addressed *in silico*, allows the interactions of such effects to be predicted, and allows the resulting additive, synergistic, or antagonistic effects and their sensitivities to be determined.

2. Global Stressors

2.1. Nutrient Loads. People pollute. By 2050, the human population is projected to be nearly 10 billion, a 30% increase over current population estimates [15], with megacities (>10 million people) largely concentrated in China as well as in other parts of Asia and Africa, most of which are along coastlines [16]. However, as the world continues to urbanize, sanitation has not kept pace; more than one-quarter of the world's population still lacks basic sanitation [17]. In the developed world, as sewage treatment processes and discharges have significantly changed in many coastal cities, evolving from none to primary, secondary, and tertiary treatments, nutrient quantity and quality discharged to local waters have changed accordingly [18, 19].

To support the population and its required food supply, the global use of nitrogen- (N-) based fertilizer, which has increased approximately 9-fold since 1970, will continue to rise [20–22]. The use of phosphorus- (P-) based fertilizers

is also predicted to increase but not as steeply as that of N [20, 23, 24]. The industrialization of farming and the rapid pace of development of concentrated animal feeding operations further accentuate this trend, as wastes from these systems are often spread on fields and at rates higher than those of commercial fertilizer ([25] and references therein, [26]).

By 2030, 93% of all rivers will have been affected by dams [27, 28]. Dam and reservoir construction and other in-river consumptive uses alter nutrient delivery, as P is retained in rivers more so than N [29]. Changes in silica (Si) availability also occur due to sediment trapping and elemental transformations following the construction of dams (e.g., [30–32]). Dams drastically reduce sediment supplies to coastal zones and greatly change the conditions for biological production and respiration in coastal environments in terms of water turbidity or clarity. Such changes in the ratio of inorganic nutrient vs. particulate organic carbon (C) alter the natural metabolic balance toward autotrophy and push coastal waters to be more eutrophic, which makes them prone to the development of bottom hypoxia. Collectively, it is increasingly recognized that altered flow and other human activities have substantially modified nutrient export (Figures 1(a) and 1(b)) in terms of total loads and proportions. These changes can create conditions where downstream assemblages across all trophic levels may change in composition.

2.2. Hypoxia and Harmful Algae. Hypoxia, a decline in water column dissolved oxygen (DO) concentrations (most researchers consider hypoxia as <2 mg/L, while some define it as <3 mg/L), is well recognized as a consequence of elevated nutrient loads and the associated enhancement of phytoplankton growth [33–35]. Long-term declines in oxygen in coastal waters have been documented globally over the past decades ([10, 36]; Figure 1(c)). Reduced oxygenation in deeper waters can also result from enhanced stratification that results from increases in river flow and warming waters [37, 38]. Warming temperatures lead to declines in oxygen directly through declines in oxygen solubility and indirectly through increases in the rate of respiration. As a consequence, hypoxia will continue in a warming world even if nutrient load reductions are met [39, 40].

There is also strong evidence that changes in nutrient loads and eutrophication are among the major causes of the global expansion of HABs [41–44]. HABs are a global phenomenon (Figure 1(d)), with an increasing abundance, frequency, and geographic extent worldwide, with new species being documented in new areas (e.g., [41, 42, 45, 46]). The expansion of HABs also contributes to hypoxia as blooms decline and decay. Well-documented examples illustrate an increase in some HABs in relation to increases in N and/or P loading [3, 41]. The historic view of phytoplankton responses to eutrophication—that is, increased nutrients promote increased chlorophyll and high-biomass blooms, leading to oxygen deduction and losses in habitat—is too simplistic for understanding why specific taxa, including HAB taxa, respond to changes in nutrients. Alterations in the composition of nutrient loads (ratios and forms) have been correlated with shifts from diatom-dominated to flagellate-dominated algal assemblages in many regions [3, 43]. Moreover, considerable emerging evidence has shown that nutrient proportions and forms have effects on toxin production (e.g., [47–50]). These toxins may kill fish or shellfish directly, or the proliferation of HABs may be harmful in ways that do not involve toxins directly. For example, blooms may disrupt ecosystem functioning by altering habitat through a reduction in light penetration or may have detrimental effects on trophic transfer due to a decline in food quality. Moreover, these effects may vary depending on the specific organisms involved. Quantifying such effects alone is challenging, and parameterizing such effects for models is even more challenging.

2.3. Warming and Stratification. Coastal and marine waters have been warming in recent decades, and further warming is expected in the future (e.g., [1]; Figure 1(e)). Warming trends result not only in changes in seasonal mean average temperatures but also in the number of warm nights, record high temperatures, heat waves, and changes in precipitation patterns [51, 52]. Higher temperatures promote increased water column stability and a shallower mixed layer depth, which in turn alter species distributions [53]. At higher temperatures, water becomes less viscous, favoring cyanobacterial species that can control their vertical position through internal buoyancy regulation and selecting against diatoms or other larger-sized taxa that sink faster [54]. In marine waters, this increased stratification may also favor flagellates that can swim to obtain their requisite nutrients from deeper waters or that can obtain their nutrients through the acquisition of particulates (e.g., [55, 56]) (Figure 3(a)).

With enhanced stratification, there is a reduced flux of nutrients to the surface, thus potentially reducing further phytoplankton growth. This reduced flux, combined with warmer temperatures, should favor the success of phytoplankton that are more dependent on regenerated sources of N and less dependent on NO_3^-, including cyanobacteria and dinoflagellates [57], thus new production should decline. These changes also alter the magnitude of the biological pump and the sequestration of C in deeper waters (Figure 3(a)).

Warming may also impact the size distribution within phytoplankton communities. Warmer waters are thought to favor smaller-sized cells because small cells may more efficiently harvest light and nutrients and maintain their position in the euphotic zone [58, 59]. Warmer temperatures can lead to decreased elemental demands for N and P for an individual cell due to the higher efficiency of enzymes and thus the potentially decreased demand for proteins and RNA that may promote a decrease in cell size [60]. Smaller phytoplankton (such as picoplankton) can, in turn, be food for mixotrophic plankton (mixoplankton). Based on paleoclimate change events, diatoms have undergone size changes, with smaller cells consistently associated with periods of warming (e.g., [61, 62]). However, Peter and Sommer [63] showed that the effect of temperature on cell size is mediated by nutrient limitation; the slopes of the temperature-size relationship became more negative as nutrient stress increased, and cell sizes did not significantly
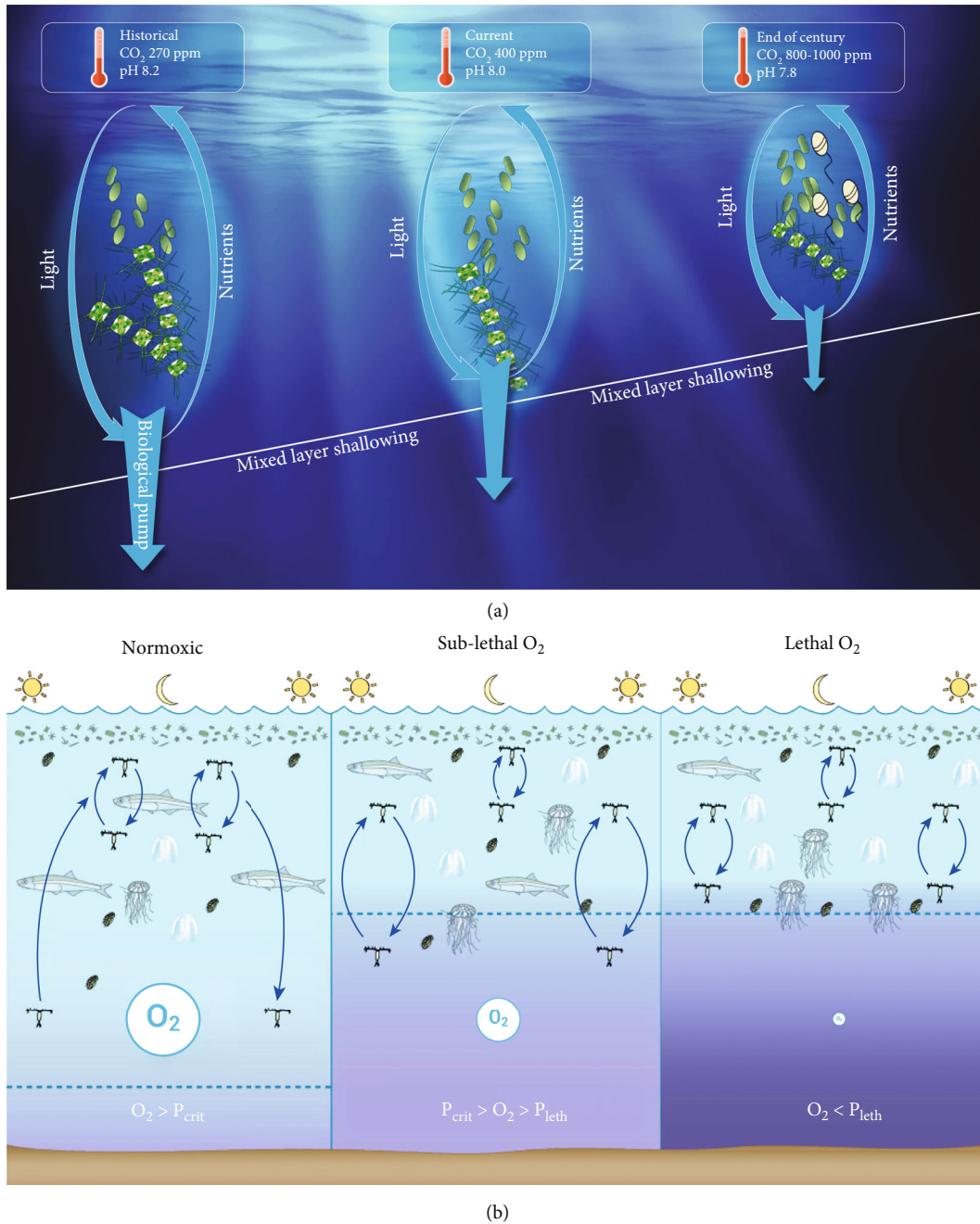
(a)

(b)

FIGURE 3: Multiple stressors with ocean depth. (a) Global change effect on the surface oligotrophic ocean, including rising temperatures and atmospheric CO_2 levels, resulting effects on pH, shallowing of the mixed layer due to increased thermal stratification, lessening of nutrient availability but increased light availability, and the changing proportion of dominant cells in the euphotic zone. Note that an increased abundance of small-sized cells and mixotrophs is projected. (b) Conceptual diagram of food web changes that may occur over diel cycles between normoxic conditions (left), sublethal deoxygenation conditions (middle), and lethal conditions (right). The size of the symbol for O_2 and the color indicate the relative amount of dissolved oxygen under each condition (with light blue indicating high oxygen concentration and purple indicating lower oxygen concentration). (a) is reproduced from Glibert [70] and redrawn and modified from Basu and Mackey [71], and (b) is modified from Roman et al. [65]; both are under Creative Commons licenses. Symbols are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (http://ian.umces.edu/symbols/).

change with temperature under the lowest level of nutrient stress. The effect of warming may also be complicated by the level of CO_2. For example, Tortell et al. [64] observed a shift to larger diatom cells (from small pennates to large chain-forming centrics) as CO_2 increased.

Warming, increased stratification, and reduced oxygen in deeper waters collectively have effects that propagate through the food web. Copepod survival, growth rates, egg production, and ingestion rates all decline as DO declines ([65] and references therein). Vertical migration behaviors

may also be disrupted (Figure 3(b)). Furthermore, smaller copepods seem to thrive under low DO more than larger zooplankton, a finding documented in several laboratory experiments (e.g., [66, 67]). Low oxygen waters may favor jellyfish over planktivorous fish because of the higher oxygen requirements of fish. Fish are also impacted at various life stages both directly and indirectly due to changes in food web structure. They are most susceptible to the effects of hypoxia during their egg and larval stages [68]. DePasquale et al. [69] showed that young silverside larvae were affected to a greater degree under conditions of low DO and low pH; the effects were greater than would be predicted from summing the effects of individual factors.

The specific characteristics of water bodies and stratification also affect the stress imposed on zooplankton and fish. If stratification results in strong temperature gradients, animals may find refuge for at least part of the day, whereas if the temperature gradient is weak, the loss of habitat is more severe ([65] and references therein). A combination of warming and increased hypoxia is thus hypothesized to lead to both smaller phytoplankton and smaller zooplankton. This shift would have direct consequences for the upper trophic level organisms that depend on plankton for food, as it would change their nutritional quantity and quality. Warming also changes habitats and thus large-scale distributions, e.g., the observed northern shift in many marine species on the US Northeastern Continental Shelf (e.g., [72]).

Other trophic interactions are affected by temperature. For example, viruses may increase their growth under warmer temperatures, leading to the possibility of greater viral infection in a natural community. In terms of bacteria, the effect of temperature on growth rates is a function of the availability of organic C. If viruses and viral lysis are stimulated by warming, the rate of supply of organic C will increase [73]. Thus, the microbial web of interactions is also complicated and affected by these stressors.

2.4. CO_2, Acidification, and Basification. Atmospheric CO_2 may rise to over $800\,\mu$atm by the end of the century, representing a 2-fold increase over current levels, if fossil fuel combustion continues to increase and if there is no human intervention (e.g., geoengineering actions to remove CO_2 [74]). This increase has already led to continued alterations in oceanic carbonate chemistry. With increasing CO_2 (and associated increases in HCO_3^- and H^+), the concentrations of OH^- and CO_3^{2-} decline (e.g., [75]). Continued decreases in the pH of the ocean can be expected [1]. The inorganic C dynamics of estuaries are more complex than those of the ocean; however, a mixture of responses to eutrophication, riverine chemistry, benthic exchange, and ocean mixing (in addition to CO_2 increases) may lead to muted pH trends or even basification trends [2]. The responses of the aquatic community to changes in CO_2 are particularly complex. While ocean acidification (OA) is accepted as a common response in the oceans, the changes in the C cycle of the oceans have many dimensions.

Ocean warming alters the equilibrium and dynamics of the marine carbonate system and can accelerate OA effects due to nonlinear nature of adding or removing CO_2 from

various sources and sinks [76, 77]. Nearshore, the effects of rising CO_2 are further complicated by inputs of nutrients and organic C from land and groundwater, which support water-column productivity (e.g., [78–81]).

Increasing OA should disproportionately stress organisms that are pH sensitive. Increasing levels of CO_2 may thus favor algae that depend on diffusive CO_2 rather than HCO_3^- as their C source or those that downregulate their C concentrating mechanisms (CCMs) and therefore reallocate energy to different pathways [82, 83]. Shifts in pH due to increased CO_2 may also alter the habitat for HABs. As pH declines, there is some evidence that cyanobacteria can outcompete eukaryotic algae; furthermore, laboratory studies suggest that some cyanobacteria experience increased growth rates under such conditions ([54] and references therein).

Decreasing pH may also alter harmful algal characteristics. For example, faster swimming speeds and downward velocities [84] and dispersive swimming behavior [85] have resulted from lower pH, potentially decreasing encounter rates with nutrients and predators. Changes in HAB toxicity have also been linked to decreasing pH and/or increasing partial pressure of CO_2 (pCO_2) [86–89].

Iron and other trace metals are important trace nutrients for the growth of phytoplankton. The speciation of metals as free metals or metals complexed with inorganic and organic ligands is pH dependent. Therefore, increases in ocean CO_2 and decreases in pH can affect metal availability or toxicity to phytoplankton growth and thus affect phytoplankton community composition [90–92].

2.5. Interactions of Effects. The combination of warming, hypoxia, and OA (and their impacts) is already occurring in many coastal systems [93]. Flynn et al. [94] showed, in a laboratory study, that the competitive outcome of different phytoplankton taxa varied with varying combinations of nutrients and pH changes. Changes in nutrient availability, form and proportion, food availability, food quality, community structure, habitat availability, size distributions are to be expected, but how these effects are manifested in populations and food webs are complex [95–97]. For example, elevated pCO_2 has been suggested to narrow the thermal window of marine heterotrophs and can limit the metabolic scope and DO carrying capacity [98]. Increased pCO_2 can also alter the food quality of herbivores by inducing shifts in species composition and succession [99, 100] as well as toxin concentrations in phytoplankton [89, 101] and by affecting the nutrient stoichiometry of organic matter. An important consideration is the ability (or lack thereof) of some microbes—as well as larger heterotrophs—to adapt to new CO_2 (or other) conditions with multigenerational exposures (e.g., [102, 103]). Irwin et al. [104] suggested that phytoplankton species niches are not stable but rather evolve in response to environmental changes on a time scale of <15 years. They emphasize that while data may show an ability for phytoplankton species to adapt on a decadal scale, little is known about their ability to adapt to larger changes on longer scales and about which traits are more adaptable.

Beyond the intuitive and direct responses, eutrophication and CO_2 enrichment alter our perspective of OA in

some unexpected ways, especially in nutrient-impacted coastal and estuarine systems. Several examples are presented next, illustrating how these stressors affect aquatic communities in several different types of systems.

3. Case Studies of Multiple Stressors and Their Complexities

3.1. Case Study 1: East China Sea. Among the most spectacular examples of the association between nutrient loading, hypoxia, and HABs is the East China Sea, which is in the region formed by the convergence of the Yangtze (Changjiang) River plume and the Taiwan Warm Current [105–107] (Figure 4). This region is warming rapidly, several times the global average, with the largest increases in temperature in winter [108]. The watershed of the Changjiang area is the most developed in China, with over 440 million people [109], and it has an annual dissolved inorganic N (DIN) load from coastal waters influenced by the Changjiang River that is higher than the DIN loads from the Mississippi or Amazon Rivers [110].

Hypoxia was first reported in the late 1950s and became a substantial problem beginning in the 1980s [111, 112] as blooms expanded. Massive blooms and massive hypoxic zones up to 10,000-15,000 km^2 in areal extent now occur regularly [105, 109, 113]. Although diatoms are still the dominant phytoplankton group, blooms of the dinoflagellates *Prorocentrum donghaiense* and *Karenia mikimotoi* are common and have been linked to fish and shrimp mortality with considerable economic consequences. The rapid increase in the export of N and P from the expansion of fertilizer use in the Changjiang River watershed has been strongly associated with the expansion of these blooms [105, 106]. However, there is considerable complexity in how nutrient export leads to blooms. Blooms form when the N-rich Changjiang River plume mixes with upwelled water from the Taiwan Warm Current, which is comparatively P-replete [114, 115]; the result is a front where the N: P ratio is suitable for growth [109]. Based on data synthesized for the period from 1970 to 2010, blooms occur when the molar ratio of total N: P exceeds 30 (Figure 4). High total suspended sediment reduces light and production in the immediate plume region, and the highest chlorophyll *a*—and hypoxia—is observed in the transitional regions between the suspended sediment front and the edge of the freshwater plume [107]. The region is also undergoing OA, and the differences in the trends in pH are apparent when the value in the recent decade is compared with that of decades ago, and these trends are accelerating with hypoxia [116, 117].

Several factors suggest that HABs and hypoxia will persist well into the future. Große et al. [112] estimated that N loading reductions of 50% will be required to reduce the extent of hypoxia. While massive N reductions have a high potential for mitigating blooms and hypoxia (Figures 4(k) and 4(l)) [112], Wang et al. [118] showed that because nutrients in China's coastal systems originate from agriculture, aquaculture, industry, and wastewater and, due to the fundamental differences in the biogeochemical cycling of N and P,

reductions in N are—and will be—exceedingly difficult to achieve, regardless of the scenario.

3.2. Case Study 2: West Florida Shelf. Waters of the West Florida Shelf, Gulf of Mexico, have been warming at a rate of ~0.18°C per decade since the early 1980s [120], and Florida's coastal estuaries follow this pattern [121]. Recent climate downscaling projections suggest that the West Florida Shelf, which is a ~900 km long and 25-250 km wide region off the west coast of Florida, will experience the most rapid warming along the U.S. East and Gulf Coasts, with the projected temperature increasing from 2.0 to 4.0°C by 2100 depending on the future emission scenario that is applied [122, 123]. This increase is expected to alter the trajectory of the Loop Current, weakening it, which would enable the surface waters near the coast to warm even more.

Due to the reduction in DO solubility and increase in water column stratification that are expected to occur, more severe hypoxia and acidification will occur in the northern Gulf of Mexico based on modeling studies [40] and observations. In terms of the hypoxic area, its annual recurrence, and the resulting OA, the West Florida Shelf is not as notable as its neighboring northern Gulf of Mexico [124]. However, in terms of HABs, the West Florida Shelf has a more persistent problem.

Blooms of the toxigenic harmful dinoflagellate *Karenia brevis* have been documented on the West Florida Shelf dating back centuries, and they occur roughly annually ([44] and references therein, [125]). However, the magnitude and duration of these events can vary from months to years and can reach up to 1000 km on the coastline and impact multiple coastal states. Physical drivers and nutrients are important for the initiation, development, and maintenance of *K. brevis* blooms (reviewed in [126]). Brevetoxins, toxins associated with *K. brevis* blooms, have caused widespread mortality events [127–129]. Brevetoxins are also known to injure humans through ingestion of contaminated seafood, dermal contact, or respiration of aerosolized brevetoxins [130–132]. On an annual scale, blooms of *K. brevis* typically initiate offshore and may be transported to the West Florida Shelf via moderate upwelling [133, 134]. Generally, *K. brevis* densities start to increase in late summer following the wet season [135] and can remain high during fall and winter when the surface water temperatures can be as low as ~15°C. Cell densities tend to decrease during late spring and rarely persist through the hot summer when temperatures are higher than 30°C [136]. Extreme bloom conditions occur only occasionally, as exemplified by the recent bloom of 2020-2021, when high cell abundances were observed throughout the year (Figure 5(a)). These blooms can be sustained throughout the summer months, at least during some years, implying that higher summer temperatures are not an obstacle to sustaining blooms. The most recent *K. brevis* bloom, initiated in November 2020 following Hurricane Eta, was sustained through the summer of 2021, with fish mortality measuring hundreds of tons. The strength of this bloom, especially during the spring and summer of 2021, may also have been augmented by a nutrient pollution spill in April 2021. A recent study suggested that over the past
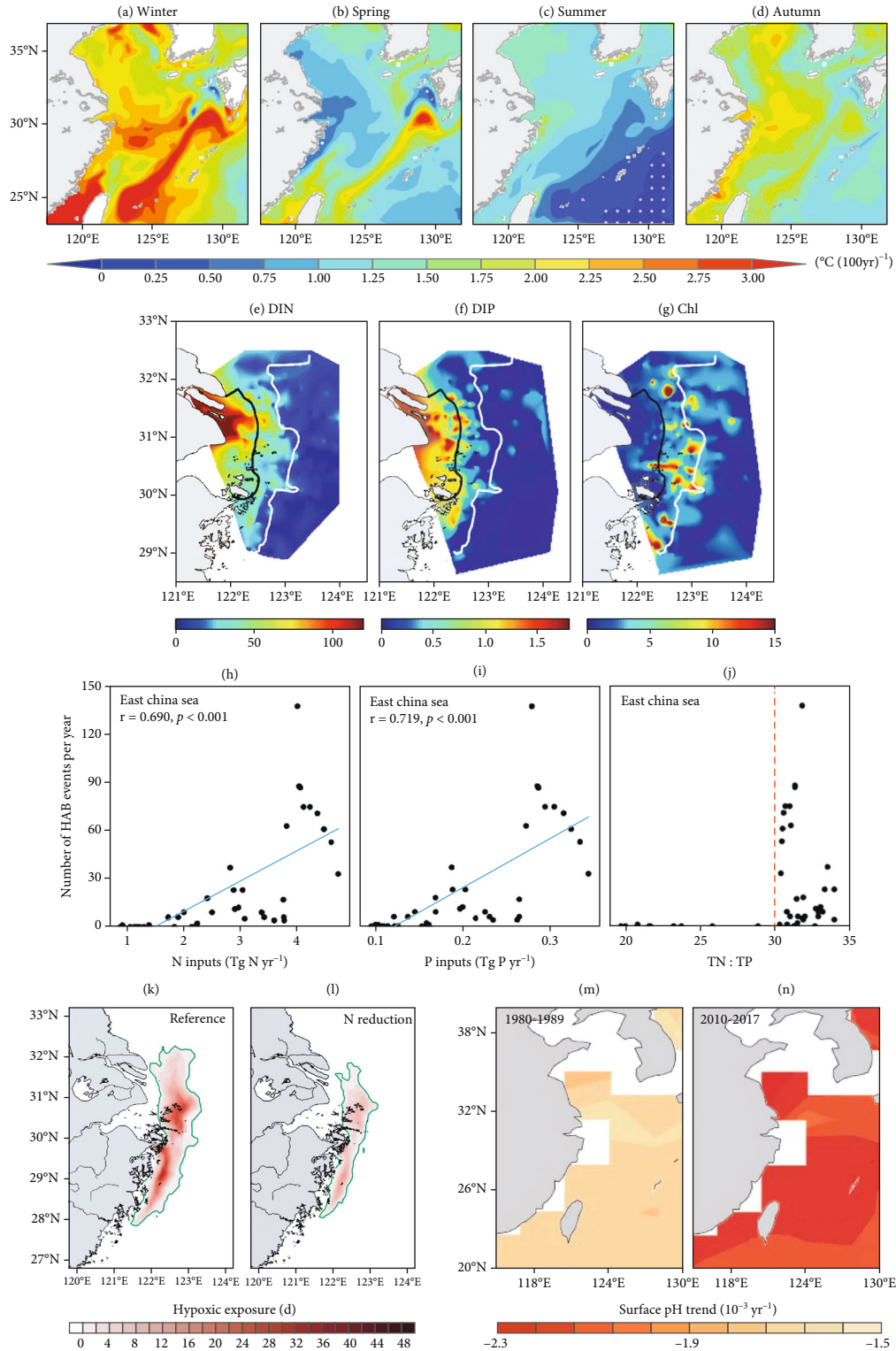
FIGURE 4: Composite of multiple stressors in the East China Sea. (a–d) Modeled linear sea surface temperature trends by season; (e–g) dissolved inorganic N and P (μM) and chlorophyll a (μg L^{-1}) based on multiyear observational data from 1988 to 2016; (h–j) number of HABs per year in relation to N and P inputs and the molar TN: TP ratio for the period from 1970 to 2010; (k, l) the hypoxic exposure (days) in the bottom layer from July to November averaged over 2008–2013 for a reference simulation and for a scenario of 50% reduction in Changjiang River N loads; (m, n) the spatial distributions of the decadal mean trend in the ocean surface pH for the years 1980-1989 and 2010-2017. (a)–(d) are modified from Sasaki and Umeda [108] and modified with permission of the American Meteorological Society; (e)–(g) are modified from Li et al. [109]; (h)–(j) are modified from Wang et al. [118]; (k) and (l) are modified from Große et al. [112]; (m) and (n) are modified from Zhang and Wang [119]; all are under Creative Commons licenses.

Karenia brevis (cells/liter)

- ⬤ (grey) Not present/background (0-1,000)
- ⭕ (white) Very low (> 1,000 – 10,000)
- 🟡 Low (> 10,000 – 100,000)
- 🟠 Medium (> 100,000 – 1000,000)
- 🔴 High (> 1000,000)

(c)　　　　　　　　　　　　　　　(d)

(e)

○ $p\mathrm{CO}_{2\mathrm{air}}$ (Mauna loa)
● WFS-N $p\mathrm{CO}_{2\mathrm{sea}}$
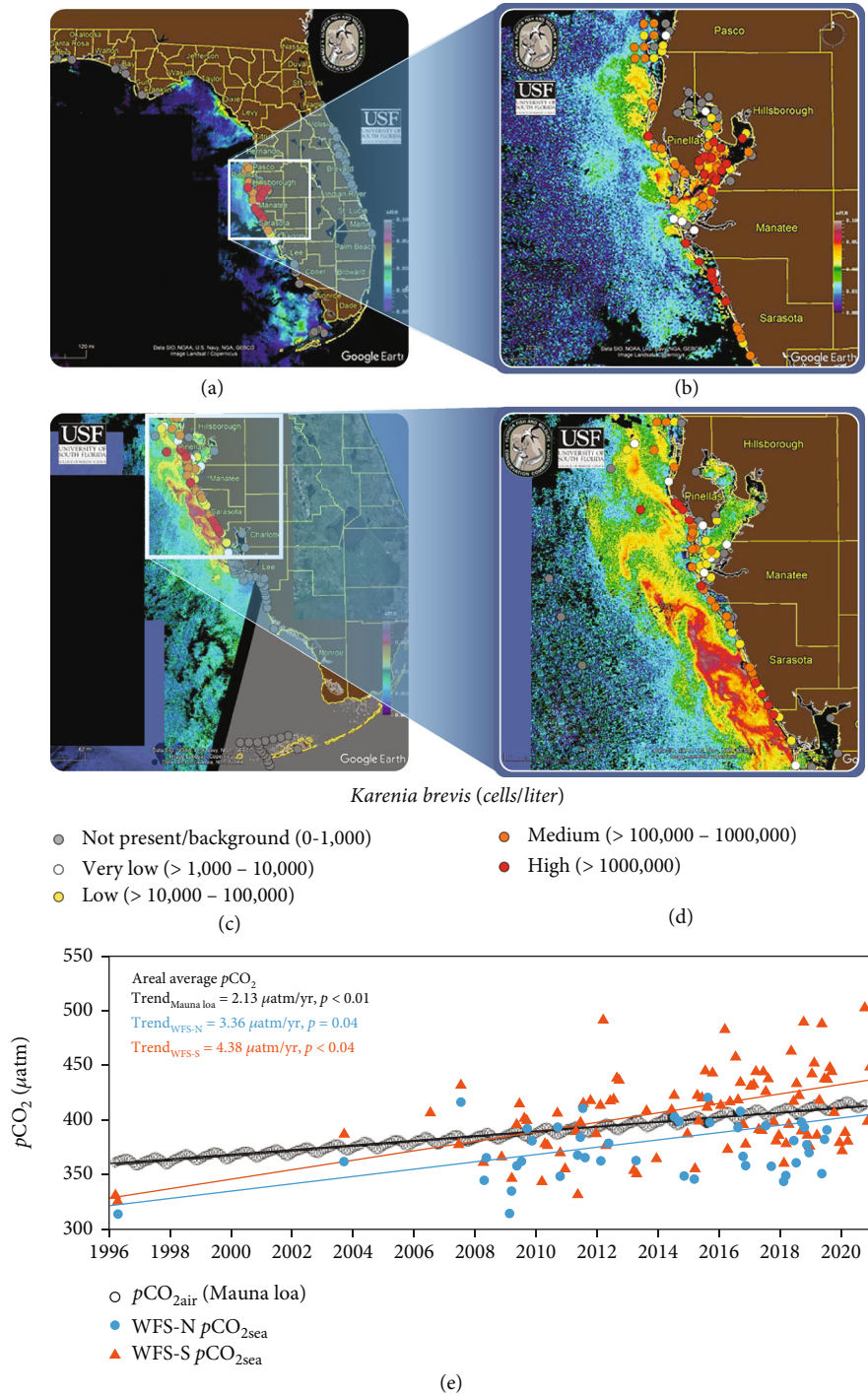▲ WFS-S $p\mathrm{CO}_{2\mathrm{sea}}$

FIGURE 5: Composite of multiple stressors in the West Florida Shelf (WFS). (a, b) *Karenia brevis* abundance in July 2021 on the West Florida Shelf and regionally in Tampa Bay; (c, d) *K. brevis* abundance in October 2021 on the southwest Florida Shelf and regionally in Tampa Bay; (e) $p\mathrm{CO}_2$ increase rates in two subregions of the WFS (north and south) and in the atmosphere. Note that the sea surface $p\mathrm{CO}_2$ increase rates (3.36-4.38 μatm yr^{-1}) in the southern region are much faster than those in the atmosphere (2.1 μatm yr^{-1}). (a)–(d) are modified from the Florida Fish and Wildlife Research Institute [144], and (e) is from Cai et al. (unpub. data).

two decades, the largest blooms occurred when hurricane events followed drought periods during the transition periods in the El Niño Southern Oscillation (ENSO) index [137]. Temperature and OA can also interact to promote *K. brevis* blooms. Laboratory studies have shown increases in the growth rates of *K. brevis* with elevated $p\mathrm{CO}_2$ [138]. Acidification may also increase toxin production in *K. brevis*, as toxin content increases with increasing $p\mathrm{CO}_2$ levels [89].

In addition to the rapid rate of warming, a 26-year survey of the changes in $p\mathrm{CO}_2$ in Florida coastal waters and

estuaries revealed higher rates of OA than those observed for the open ocean [139] (Figure 5(b)), presumably because eutrophication, land use changes, and watershed inputs are enhancing acidification. Increased stratification will also enhance respiration-induced acidification, an effect that may be enhanced by larger freshwater flows under future conditions [40]. Thus, future changes in climate are expected to continue to amplify acidification on the West Florida Shelf, although the northern Gulf of Mexico has been historically buffered by a high alkalinity input from the Mississippi River [140].

A recent analysis also confirmed that large HAB events on the West Florida Shelf are associated with increased deoxygenation [141]. Even with the more limited data from the West Florida Shelf relative to the amount of data available for the mouth region of the Mississippi River, it was recently documented that from 2003 to 2019, hypoxia occurred on the West Florida Shelf in 9 of these 17 years, and the greatest hypoxia was observed when extreme K. brevis blooms also occurred [141]. Unlike hypoxia in the northern Gulf of Mexico, which is typically confined to bottom waters, the vertical extent of hypoxia on the West Florida Shelf covers more of the water column, likely affecting some fish, such as grouper [142]. In the bloom of 2005, when hypoxia was recorded, gag grouper was found to have suffocated [143]. Again, in 2014, a fish survey on the West Florida Shelf documented dead and moribund fish, most of which were found to be red grouper, associated with a low DO event resulting from a bloom of K. brevis that had occurred in the area [142]. Thus, for K. brevis blooms, fish death may result directly from toxins and from HAB-induced hypoxia. When waters are warm, especially during unusual but increasingly more frequent summer blooms, the compound stress of heat and hypoxia may make fish more susceptible to toxicity.

3.3. Case Study 3: US Mid-Atlantic Estuaries. Estuaries are particularly complex with regard to the effects of multiple stresses. The very nature of these systems, where physical and chemical changes result from substantial interactions with watershed inputs, the adjacent ocean, and sediments, suggests more variable environments. Temporal fluctuations in pH, oxygen, temperature, and primary production can be extensive, leading to more extremes and variability [145]. Compared with the open ocean, coastal and large estuarine systems are experiencing an accelerating pace of acidification as organic matter respiration contributes to dissolved organic C production, in addition to atmospheric CO_2 [2, 116, 146]. However, CO_2 declines are driven by high primary production, which occurs during the development of high biomass blooms. Such high biomass can lead to an elevated pH (basification) due to CO_2 drawdown, countering the effects of OA. Then, as high biomass blooms decline and decay, enhanced rates of respiration follow, in turn leading to a declining pH, which may be augmented in estuaries with a lower buffering capacity. Accordingly, given the difference between river and ocean end members, strong seasonal, horizontal, and vertical spatial gradients in total alkalinity (TA), dissolved inorganic C (DIC), pCO_2 and pH develop in estuaries [147–149].

The largest estuary in the continental US, Chesapeake Bay, illustrates why understanding multiple stressors in estuaries is so complex. The bay receives large amounts of nutrients from sewage effluent and from nonpoint sources, mainly agricultural and urban runoff as well as atmospheric deposition, all of which contribute to excessive phytoplankton production and hypoxia [150, 151] (Figures 6(a) and 6(b)). As a consequence of eutrophication and N loading from the watershed, Chesapeake Bay has experienced hypoxia and has suffered from major HAB problems for decades (e.g., [152–156]) (Figures 6(c)–6(e)). Moreover, the native oyster populations have collapsed, and shifts in fisheries have occurred due to fishing pressure, loss of habitats, and declining water quality (e.g., [150]).

Chesapeake Bay also illustrates the spatial and temporal complexity of C chemistry in dynamic eutrophic estuaries. The bay is commonly divided into three major sections: an oligohaline, heterotrophic upper bay; a mesohaline, generally autotrophic midbay, containing most of the hypoxic zone [157]; and a polyhaline lower bay with a nearly balanced net metabolism [158]. The upper bay generally displays net heterotrophy due to high turbidity and inputs from CO_2-rich riverine waters, while the mid to lower bay regions display net autotrophy and a bay-wide shift from net autotrophy in winter-spring and fall to net heterotrophy in summer [159]. Each of these bay regions has a distinct C chemistry regime. In the upper bay, where the pH in near-surface waters has historically been low due to the low pH of the incoming river water, there has been a long-term basification trend, influenced by changing freshwater input and increased total alkalinity from the Susquehanna River (Figure 6(f)) [160]. In contrast, in the lower bay, which has historically had a higher pH, modeling suggests a multidecadal decrease in pH and acidification due to oceanic influence and possible changes in primary production (Figure 6(g)). The counterbalance between OA and river basification [161] results in the most variability in the pH and carbonate chemistry in the autotrophic midbay [162], with strong pH fluctuations driven by phytoplankton photosynthesis. Additionally, seasonally, calcium carbonate dissolution is an important buffering mechanism for bottom water pH changes in late summer in the midbay, leading to higher pH values in August than in June despite persistent hypoxic conditions during the summer [146, 163, 164]. Wind-driven lateral upwelling can advect deep water with low pH onto shallow shoals and reduce the aragonite saturation state, potentially exposing a large fraction of oyster beds in the main stem of the bay to undersaturated carbonate mineral conditions during wind events [165, 166].

Extrapolating these effects beyond Chesapeake Bay to other estuaries is complicated by coastal topology, retention, and latitude [167]. Dürr et al. [168] defined four major types of near-shore coasts, including small deltas, tidal systems, lagoons, and fjords, based on hydrological, lithological, and morphological criteria. These systems represent the estuarine filter, where riverine waters mix with those of the coastal ocean and a complex interplay of physical and biogeochemical processes occurs. These processes, which include primary production, remineralization, burial, and
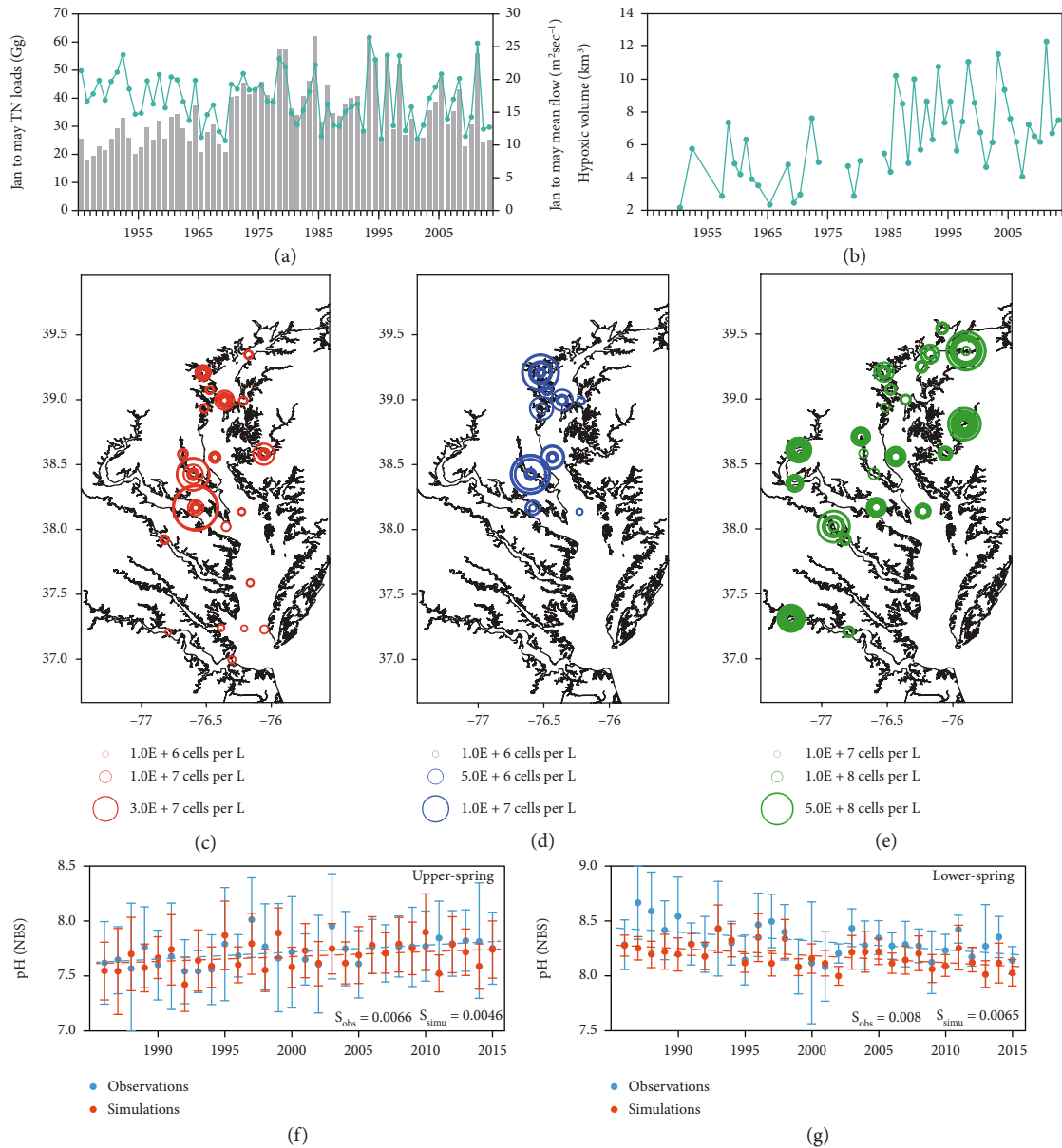
FIGURE 6: Composite of multiple stressors in Chesapeake Bay. (a, b) Time series of (a) winter-spring (January–May) flow (blue dots) and total nitrogen loading (green bars) from the Susquehanna River and (b) summer (July) hypoxic volume (defined as the DO concentration below 2 mg/L). The hypoxic volume increased two-fold between the 1950s and 1980s, corresponding to a similar increase in nutrient loading. Although nutrient loading started to level off from the 1990s, the hypoxic volume continued to increase and exhibited large interannual variations. (c–e) Examples of HABs in Chesapeake Bay based on long-term data. (c) represents *Prorocentrum minimum*, (d) represents *Karlodinium veneficum*, and (e) represents cyanobacterial HABs. (f, g) The pH trends with time for upper and lower Chesapeake Bay in spring. (a) and (b) are modified from Li et al. [151], (c)–(e) are modified from Li et al. [154], and (f) and (g) are modified from Shen et al. [161]. (a)–(e) are reprinted with permission of Elsevier; (f) and (g) are under a Creative Commons license.

denitrification, may significantly alter riverine nutrient delivery to continental shelves [169]. Compared to Chesapeake Bay, the nearby Delaware Bay has no hypoxia and has limited acidification and HABs due to consistent vertical mixing and ocean exchange. This result underscores the role of the physical setting in determining a system's vulnerability to stressors. The shallow coastal lagoons of Maryland's Coastal Bays and Delaware's inland bays provide further contrasts. They have spatially limited but localized diel cycling hypoxia and acidification, as they are shallower,

and biogeochemical interactions with the benthos become more important in these shallow systems, as do high frequency changes in CO_2, pH, and nutrient fluxes [170]. Retentive zones are also important for HABs, especially those that form cysts, as the cysts accumulate and can lead to blooms whenever favorable conditions occur. Shallow, enclosed coastal lagoons are thus subject to recurrent blooms once a HAB population becomes established. Fjords are particularly effective in retaining nutrients with characteristic residence times as long as decades, while small

deltas have a low filtering capacity. Estuaries in temperate regions of the Northern Hemisphere are a particularly important sink for nutrients because of the prominence of relatively long residence time tidal systems. In tropical and subtropical regions, retention is much less efficient, and a large proportion of the nutrient inputs to the ocean bypass the coastal filter by discharging directly onto the shelves in large rivers. Large rivers largely bypass the near-shore filter, while karstic and arheic coasts act as inactive filters [171].

Overall, the magnitude and effects of nutrient pollution, hypoxia, and other stressors depend not only on exports from land sources but also on coastal typology and latitude. In retentive regions, nutrients can be retained, recycled, and transformed, keeping the site in a nutrient-enriched condition. This can enhance phytoplankton accumulation, high-biomass HABs, and hypoxia.

4. Strategies for Predictive Modeling

4.1. End-to-End and Coupled Models. All of the stressors described above are linked in some way, whether directly through cause and effect (e.g., nutrient load and HABs), as a consequence of the same process causing multiple stressors (e.g., respiration consumes oxygen and acidifies water), or as both a direct and an indirect cause of stress (e.g., temperature enhances respiration, alters HABs, and imparts direct physiological stress). Consequently, there remains a critical challenge to measure the response of organisms to these diverse stressors simultaneously and also to quantitatively predict how these stressors will evolve over time and how interactions in this evolution will confer to organisms. Assessing and predicting these interactions requires coordinated modeling and experimentation.

Coupled biophysical modeling will play a critical role in the assessment of multistressors, and many well-developed suites of models for assessing the effects of water quality and habitat changes on biota have been developed for different systems [172–174]. End-to-end models are useful in representing the entire food web (including multiple species or functional groups at each of the key trophic levels as well as top predators in the system) and the associated abiotic environment. To gain flexibility to represent all environmental factors and responses and their interactions, such models are ideally built as multitrophic, coupled model systems with multiple connected modules (each its own model) that can be added or coupled as needs or questions demand (Figure 7). Models are dependent on data, of course, and the choice of a coupled modeling framework also depends on the specific needs for model application. A coupled modeling system provides the power needed to weave the connectivity between physical changes associated with climate change to variability in deoxygenation, OA, and HABs, as well as their impacts on upper and lower trophic levels, and can be sufficiently flexible to allow targeted applications. In a coupled modeling system, the outputs of one module become inputs to other modules. When land use models are coupled to food web models, integrated predictions from

river and land inputs through physics to the lower and upper trophic levels can be attained.

As nutrient loads from the watershed are a common stressor to many aquatic systems (watershed box in Figure 7), various hydrological models have been developed to estimate nutrient loading, such as the Spatially Referenced Regressions on Watersheds (SPARROW), Soil and Water Assessment Tool (SWAT), and Nutrient Export from Watersheds (NEWS). These models take into account the broad range of nutrient sources and their alteration across the landscape. The Integrated Model to Assess the Global Environment-Global Nutrient Model (IMAGE-GNM) [29, 175], which is based on data from more than 5000 exoreic basins and includes natural sources, such as N_2 fixation and P weathering and anthropogenic sources (nonpoint inputs from fertilizer by crop type; N_2 fixation by crops, atmospheric N deposition, and manure by animal species; point sources from sewage, as estimated by human population and treatment level) [176], has recently been used to assess future global cycles of N and P and consequences for nutrient pollution of surface water by applying various societal drivers of nutrient sources [175].

More recently, basin-scale riverine nutrient and carbon inputs to bays and coastal oceans have been derived from a process-based model, the Dynamic Land Ecosystem Model (DLEM). The DLEM couples major biogeochemical cycles, the water cycle, and vegetation dynamics to simulate temporally and spatially explicit fluxes and storage of water, C, N, and selected greenhouse gases from terrestrial ecosystems to river networks and eventually to estuaries and coastal oceans (e.g., [177–179]). These fluxes are simulated through the generation of surface runoff after rainfall events, leaching of these materials to river networks, transformation of carbon and nutrients in rivers and lakes, and transport from upstream areas to coastal regions. Extreme climate events (such as flooding and drought) are identified as being primarily responsible for seasonal and interannual variations in C and N exports from watersheds. In the northern Gulf of Mexico, an attempt was made to couple the nutrient and C exports from the DLEM to an ocean physical-biological coupled to predict the dynamics of nutrients, DO, pCO_2, and pH in the coastal ocean [180].

4.2. Key Model Components for Multistressor Coupled Models. To represent the physical and biogeochemical aspects of coastal ecosystems sufficiently well to simultaneously model HABs, deoxygenation, acidification, and warming, coupled hydrodynamic and biogeochemical models are needed. Such models have been applied in systems such as Chesapeake Bay, Puget Sound, the Baltic Sea, the northern Gulf of Mexico, the East China Sea, and many other regions. All of these models share a general framework involving a highly resolved (meters to a few kilometers) physical circulation model that simulates current velocities, salinity, sea level, temperature, and mixing, and this framework is coupled in some way to a biogeochemical model that represents phytoplankton, nutrient cycling, organic matter production, consumption, and transport, and the associated variability in DO and the carbonate system (Figure 8). The
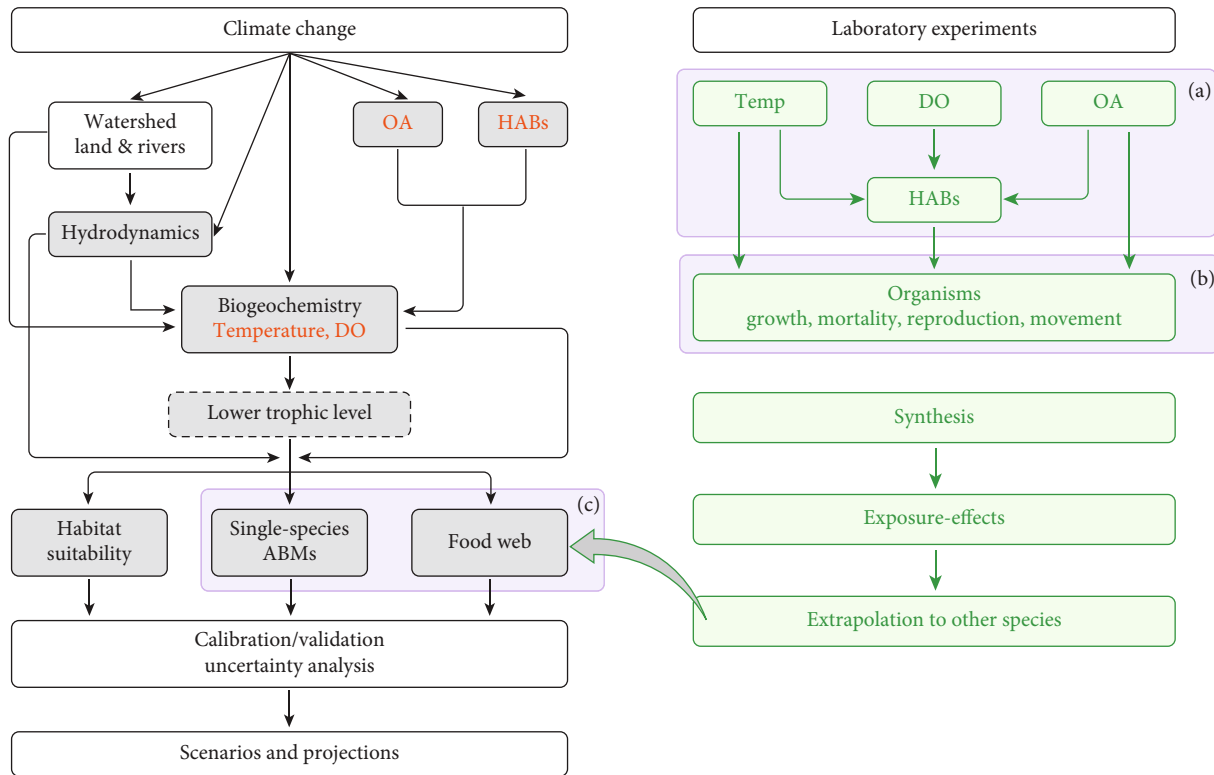
FIGURE 7: Schematic showing the major components and linkages for modeling ecosystem responses to multiple stressors. The left side depicts a coupled modeling system that links hydrodynamics, biogeochemistry, lower trophic level, and upper trophic level modules. The right side is a parallel effort with laboratory experiments to provide the exposure-effect functions to the species and functional groups in the modeling system. The lower trophic level module is shown as dashed lines because, depending on the system and availability of models, it can be a standalone module, part of the biogeochemistry module, or part of the upper trophic level module. The three major types of interactions indicated by purple boxes are where stressors are explicitly evaluated either in experiments or in the coupled modeling system. They are (a) interactions among stressors in their effects on organisms—in this case, how temperature, DO, and OA affect HABs and their toxicity; (b) direct effects of single and combinations of stressors on organisms; and (c) indirect effects of responses to multistressors arising from complex life cycles (population) and interspecific interactions (food web).

key element of these frameworks is the ability to dynamically predict key stressor variable concentrations (e.g., carbonate saturation and DO) as they respond to temperature dynamics (including warming), riverine inputs (including nutrients), and exchanges with adjacent ocean boundaries (including acidifying offshore water).

Various types of hydrodynamic models have been configured for specific systems. The Regional Ocean Modeling System (ROMS) [181] and the Finite Volume Coastal Ocean Model (FVCOM) [182] are two hydrodynamic models commonly applied to coastal and estuarine systems [183], but many other modeling systems are available. One of the primary differences in these systems is their flexibility in the shape and size of the grid used to represent the bathymetry and area of the system of interest. The more flexible the grid is, the better it may resolve abrupt changes in bathymetry (and thus simulate the true depth distribution of the system) and the fine-scale representation of shorelines and freshwater-marine transitions.

There is a larger diversity of biogeochemical models that have been applied in coastal ecosystems, given the differences in the degree of complexity and representation of bio-

logical and chemical pools. Some biogeochemical models share common features [184, 185] in that they may represent a single phytoplankton group and are limited to tracing 1-2 key constituents (e.g., N and P). Other models include organic as well as inorganic forms of N and P, and some are multistoichiometric [186, 187] and may simulate multiple phytoplankton groups. For example, the ERSEM (European Regional Seas Ecosystem) model [188] has four plankton functional types for phytoplankton (picoplankton, flagellates, diatoms, and dinoflagellates), three zooplankton functional types (microzooplankton, mesozooplankton, and heterotrophic dinoflagellates), and one bacteria functional type. The ERSEM model also parameterizes phytoplankton and bacteria with variable C: N: P stoichiometry. Biogeochemical models may fully represent sediment biogeochemistry through multiple-layer modules (e.g., [189]) or through simple parameterizations [190]. Most of these models represent DO, given the important feature of deoxygenation in coastal ecosystems, and modern biogeochemical models represent the carbonate system, but with a range of formulations, where some include calcification, dissolution, and anaerobic metabolism, while others may represent only the
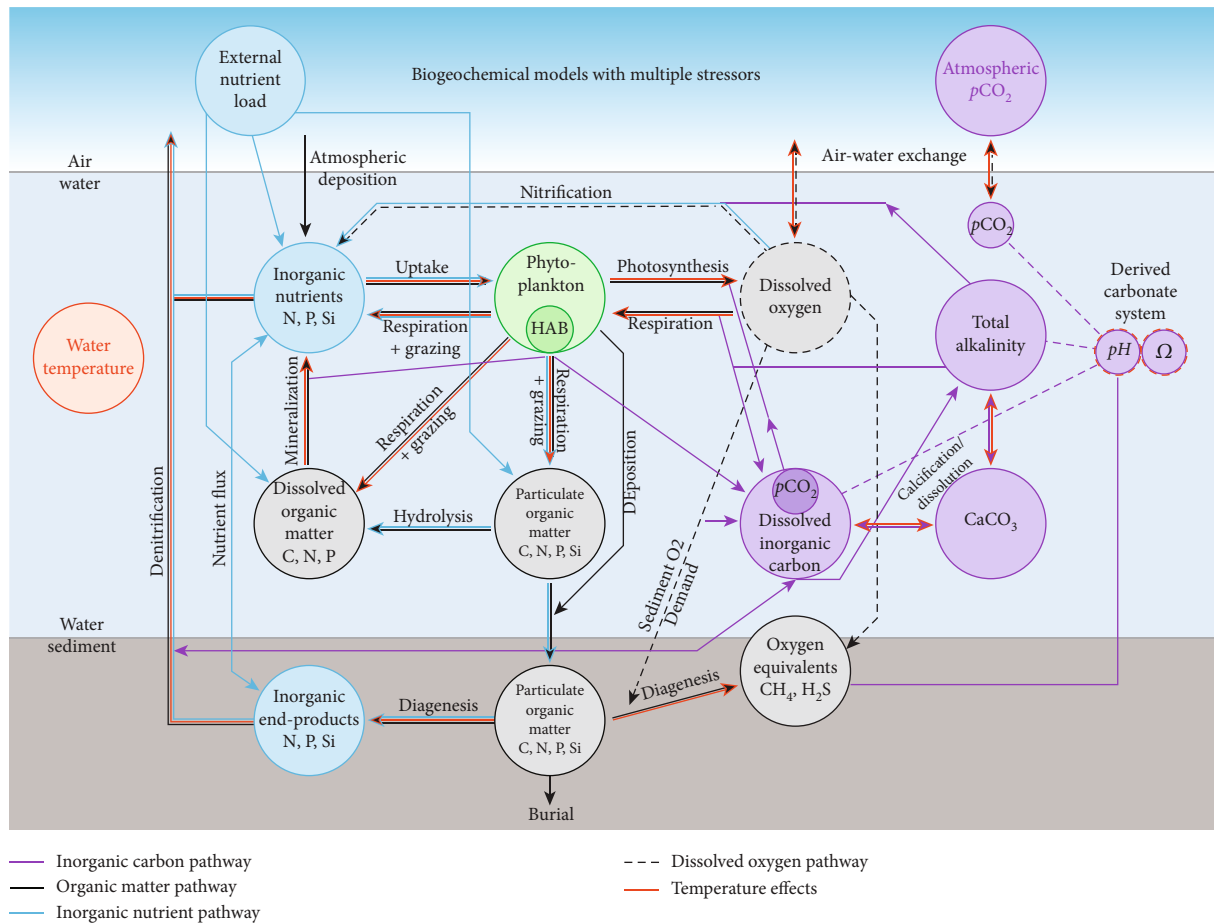
FIGURE 8: Schematic diagram of state variables, biogeochemical reactions, and interactions between stressor variables typically included in biogeochemical models. Circles represent state variables (stocks and concentrations) or external forces (temperature, nutrient loading, and atmospheric CO_2). The lines represent biogeochemical reactions (primary production and calcification) or physical exchange (air-water flux and sediment-water flux). The complexity of the diagram underscores the tight connectivity of the major biogeochemical processes as they impact nutrients, phytoplankton, DO, and both organic and inorganic carbon dynamics, as well as the ubiquitous role of temperature in modulating these processes. Colored lines represent inorganic carbon (purple), nutrients (blue), and organic matter (black) flows, while the black dashed lines represent DO-influencing flows and the purple dashed lines represent linkages between inorganic carbon variables and pH and the calcite or aragonite saturation state (Ω). No arrows are included in flows connecting pH to oxygen equivalents or TA to photosynthesis and respiration because multiple processes or solutes are involved. Red lines indicate biogeochemical processes or physical exchanges that are impacted by water temperature and therefore warming.

impacts of aerobic metabolism on dissolved inorganic C and total alkalinity (Figure 8) and often include a prediction of DO dynamics [191].

Although many of the models described above have the capability to represent the key processes and variables relevant to multiple stressors (e.g., temperature, DO, pH, and HABs; boxes in Figure 7), the capability of current and past models to reproduce reliable hindcasts and projections of these multiple stressors is variable. The first consideration for models is that stressors need to be represented so that their possible effects on each other can be simulated (e.g., warming enhances HABs and HABs cause hypoxia). Some of these linkages are relatively straightforward and commonly implemented, for example, the simultaneous impact of phytoplankton respiration on dissolved inorganic C production, DO consumption, total alkalinity balance, and thus its impact on deoxygenation and acidification (Figure 8).

Other linkages may be less commonly implemented, such as a formal representation of calcification as it occurs in the water column and sediments and how the production of calcium carbonate may be related to primary production and the fate or dissolution of the associated calcium carbonate may buffer against acidification (Figure 8) (e.g., [163]). Having all of the stressors within the same hydrodynamic-biogeochemical coupled modules is also necessary to ensure a consistent set (spatial and temporal scales) of multistressor predictions for use by a connected upper trophic level module.

Modeling HABs has other complexities. Representing the dynamics of HABs in models that also consider C chemistry has been relatively rare until recently [192]. Since HAB models target an individual species and "phytoplankton" in a biogeochemical model are modeled as generic functional groups, a common strategy is to model the HAB

individually, while the other phytoplankton are represented by the aggregate functional classes, a rhomboid strategy [193, 194]. Many HABs are mixotrophic. Thus, their growth depends not only on light and nutrients but also on prey availability, in addition to changes in inorganic C. An example of adding mixotrophic HABs to a biogeochemical model is the model by Li et al. [195]. This submodel describes the C-N-P-based interactions within a mixotroph cell (Figure 9) and builds upon the "perfect beast" model of Flynn and Mitra [196]. It accounts for photosynthesis, inorganic nutrient uptake, and consumption and digestion of prey, as well as the potential contribution of photosynthesis from the incorporation of prey. As part of an idealized coupled modeling system, HAB addition to the biogeochemical module may also need to represent the toxicity of HABs to other organisms; this is an emerging area of research. The "perfect beast" model was used to explore the potential effects of temperature and changes in nutrient stoichiometry on both the mixotrophic dinoflagellate *Karlodinium veneficum* and the availability of its prey [197] and was applied to Chesapeake Bay to assess the seasonal and spatial dynamics of mixotrophy [195].

Moving up in trophic complexity to explore the responses of upper trophic levels involves a major shift in modeling approaches. Modeling approaches shift from Eulerian source-sink approaches, which are appropriate for the biogeochemical module, to structured (e.g., age, stage, or agent-based) population dynamics that represent the processes of growth, mortality, reproduction, and movement. It is often necessary to reconfigure the spatial and temporal resolutions from the physics and lower trophic level modules to the upper trophic level modules. There is often a gap between the outputs of the biogeochemical module and the needed lower trophic level information (zooplankton and benthos) for input to the upper trophic level module [172] (lower trophic level box in Figure 7). While coverage of the lower trophic levels is clearly needed, whether that belongs in the biogeochemical module or upper trophic level module remains a site-specific and model availability question. In general, NPZ (nutrient-phytoplankton-zooplankton) models are being expanded to predict the dynamics of phytoplankton and zooplankton that can be transferred to upper trophic level modules [198]. This movement toward model predictions of the lower trophic levels beyond chlorophyll, combined with consideration of how multiple stressors affect the lower trophic level species, will benefit multistressor coupled modeling efforts.

4.3. Modeling Responses. There are multiple approaches for modeling the responses of both lower and upper trophic levels to multiple stressors, including habitat suitability, agent-based population dynamics modeling, and food web modeling (Figure 7). Habitat suitability is a statistically based analysis that is closely linked to field data [199], while the other two approaches rely on the simulation of organism growth, mortality, reproduction, and movement [200]. The reliance on statistical analysis and monitoring data for habitat suitability generates results that are easier to explain and defend and that have relatively high confidence but are predictions of habitat capacity for organisms; abundance

may not respond the same way depending on the processes and life stages that limit a population [201]. Agent-based population modeling enables a detailed representation of complex life cycles, and the representation of movement of individuals provides for a realistic estimation of the exposure of mobile organisms to multiple stressors that themselves vary in time and space. Population-based approaches simplify interspecific interactions (e.g., predation and prey) to focus on the dynamics of the species of interest. Inclusion of food web modeling simplifies the process representation of each population to enable an explicit representation of how the many species comprising the food web can affect each other in their responses to multiple stressors. Each of these approaches has been used to assess stressor effects in coastal and estuarine systems.

The first approach, modeling habitat suitability, relies on empirical field data and laboratory data to predict how habitat quality, quantity, and spatial arrangement are affected by environmental changes [202]. Habitat suitability models can be applied to both lower and upper trophic levels. There are many examples of using habitat suitability to assess single and multiple stressors on estuarine and coastal fish and shellfish (e.g., [199]). Glibert et al. [203] used ERSEM output to define the habitat suitability for two HAB taxa, pelagic *Prorocentrum* spp. and *Karenia* spp., in three oceanic domains, the NW European Shelf-Baltic Sea system, NE Asia, and SE Asia. They predicted habitat changes under present-day (1980-1990) and climate change scenarios [204] for the period 2090-2100. Li et al. [205] used a similar approach for two estuarine HAB taxa, *Prorocentrum minimum* and *Karlodinium veneficum*, and estimated climate-induced variability in the hydrological forcing as a mechanism driving the interannual shifts in the algal distributions. They applied climate downscaling simulations to show how the distribution of the two species in the estuary would change under future climate scenarios. Habitat suitability is widely used to assess responses to stressors to provide management advice (e.g., essential fish habitat) because it is estimable directly from field data. Habitat suitability modeling has advanced in terms of statistical fitting and incorporation of ecology [206, 207] and is well suited to be further adapted to multiple stressors. For example, Schlenger et al. [208] applied a 3D habitat volume model to investigate the physiological tolerances of 12 fish species in Chesapeake Bay to changes in temperature, salinity, and DO.

The second approach, agent-based population dynamics modeling, allows fine detail for a single species [209]. An agent-based approach in which the model tracks individuals (agents) of a single species enables a high resolution of exposure to multiple stressors. Huebert et al. [210] illustrate this approach using an agent-based population model for winter flounder that migrate between the river/estuary nursery habitat and the shelf region of the Northeast US. They coupled a detailed submodel for the early life stages that are exposed to warming and OA in the estuary with a coarser adult submodel to simulate population dynamics during a multidecadal period that included a warming trend. They incorporated OA effects on egg and larval stages, synthesized from reported laboratory experiments (e.g., reduced egg
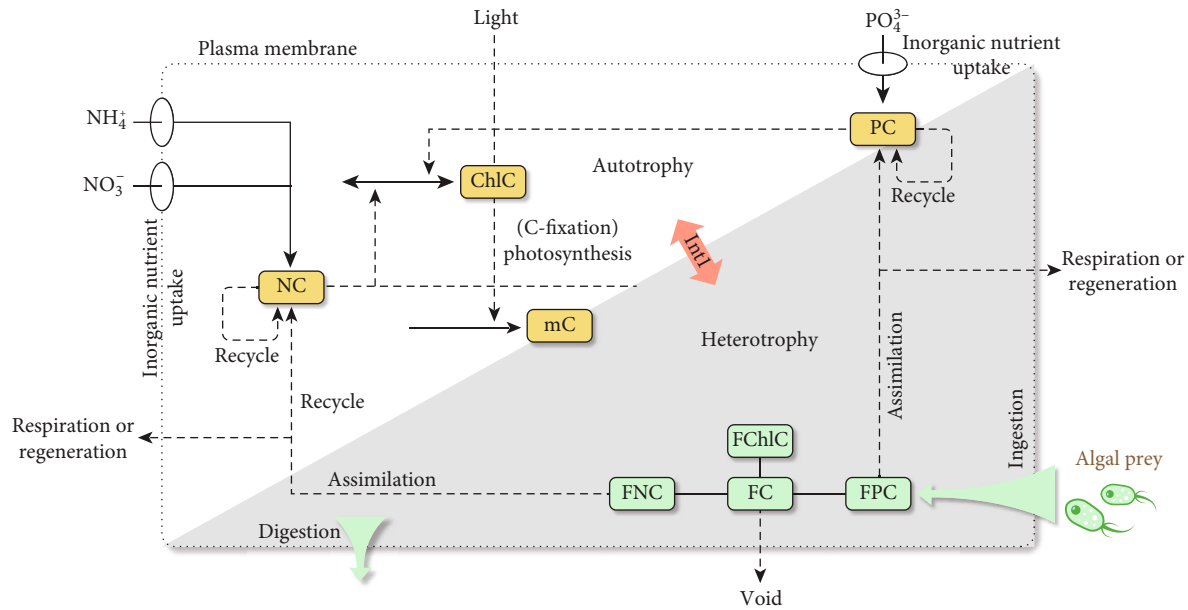
FIGURE 9: Schematic of the structure of the "perfect beast" model for mixotrophy. It shows major flows in and out of state variables (solid arrows and boxes) from the external parameters (NO_3^-, NH_4^+, PO_4^{3-}, and light) and the major feedback processes (dashed arrows) within a single mixotrophic cell. Autotrophic growth uses inorganic nutrients and light via the photosystems of the mixotroph (phototrophy; white section). Predation brings algal prey into the food vacuole within the confines of the mixotrophic cell (heterotrophy; gray section). The state variables (yellow boxes) that describe carbon (C), nitrogen (N), phosphorus (P), and chlorophyll (Chl) associated with core mixotroph biomass are mC (C-biomass of the mixotroph), ChlC (chlorophyll C quota), NC (cellular NC quota), and PC (cellular PC quota), while the same constituents (green boxes) associated with the content of food vacuole are FC (food vacuole C content relative to mC), FChlC (food vacuole Chl content relative to mC), FNC (food vacuole N content relative to mC), and FPC (food vacuole P content relative to mC). Modified from Lin et al. [197] under a Creative Commons license.

fertilization rate and slowed growth), and showed that OA amplified the negative effects of warming (synergistic ecological interaction) on long-term stock productivity. Agent-based models have also been used to assess warming (climate change) and hypoxia effects on key species [211, 212].

The third approach simplifies details on individual species but explicitly represents the species and groups that comprise the entire food web. There are many available food web models, and Ecopath with Ecosim (EwE) and Atlantis are the most commonly applied [213]. Reduced complexity food web models that highlight aspects of the food web to address specific questions also offer a viable approach [214]. Ihde and Townsend [215] used an Atlantis food web model for Chesapeake Bay to examine the responses of the food web to the individual and combined effects of multiple stressors. The model simulated the biomass dynamics of 46 species/functional groups for 50 years (repeating historical years) by dividing the bay and its river tributaries into 97 irregular polygons. Water movement was driven by the output of a hydrodynamics model, and nutrient and sediment loads were derived from a coupled watershed-airshed-estuarine system of coupled models. Stressors of marsh and submersed aquatic vegetation losses (habitat) and warming were combined with reduced N and sediment inputs from rivers expected under restoration and simulated separately and together. Changes in the biomasses of the groups (average of years 40-50) were compared to the baseline and showed that warming effects dominated the responses and

that the combined response of all stressors was more than expected from each stressor due to direct and indirect ecological interactions.

Coordinated analyses using these three complementary modeling approaches will generate more complete and robust predictions than can be obtained from each of the approaches alone. Combining single species population modeling with ecosystem modeling has also been advocated for providing robust advice for management [216].

4.4. Challenges of Data Availability. A major challenge with modeling multistressor effects is the availability of sufficient high-quality data appropriate for the model, taxa, system, and stressors of interest, let alone the effects of their multiple interactions. Indeed, many new technologies and instruments are yielding massive quantities of data regarding high temporal and spatial variations in DO, temperature, pH, pCO_2, nutrients, and phytoplankton composition and abundance. While many sampling programs may be adequate for capturing seasonal or otherwise regular oscillations in key variables or key species, the resolution is often inadequate to capture the extremes and high-frequency variations that drive the largest stressor effects. Thus, the ability to detect a stressor response may be limited. The frequency of sampling is also limited for rate measurements, including grazing (including mixotrophic grazing) and feeding rates, and data on interacting stressors at all trophic levels are comparatively scant.

One strategy is to leverage existing information on stressor effects and interactions by synthesizing available laboratory results, targeting experiments at a reduced set of stressor combinations, and then using extrapolation methods to spread the information to the full set of combinations needed by biota in the lower and upper trophic level modules (laboratory experiment column of boxes in Figure 7). There are many studies on the single direct effects of temperature, DO, or OA both on lower trophic level taxa and on fish growth and mortality [4, 210, 217], and there are some data on the interaction of pairs of temperature, DO, and OA on some species [218, 219]. Factorial experiments can theoretically provide the needed information, but the number of combinations quickly exceeds practicality. There are hundreds of possible combinations of multiple stressors affecting each other and singly and together affecting the growth, mortality, reproduction, and movement of individuals within a life stage (ecological effect interactions) for multiple life stages of multiple species.

A staged approach of using laboratory experiments to screen for stressor-stressor and direct ecological effect interactions, coupled with a fuller set of experiments that quantify growth, mortality, reproduction, and movement effects on key life stages of selected species, can be applied. Selection of the target species should consider their life history (e.g., resident, spawning, and nursery grounds) relative to the major species in the food web, their trophic role within the energetic pathways of the food web, their relevance to management such as commercial or recreational importance, and the sensitivity of their different life stages to the stressors. The experimental species can be strategically selected for their representativeness because they will be used as the basis for extrapolating stressor effects to other species. An initial set of experiments can determine whether the combined effects of exposure to multiple stressors are additive, synergistic, or antagonistic [219, 220]. Combining the results of experiments with the effects reported in the literature can lead to estimates of exposure-effect functions (response surfaces [221]) that relate the levels of each of the stressors to growth, mortality, reproduction, and movement [222, 223]. Methods of extrapolating stressor experiments used in ecotoxicology can then be used to extrapolate the exposure-effect functions measured on one species to other unmeasured species [224, 225].

The use of the suite of coupled models envisioned here for assessing multistressors will present new challenges to model validation and the assessment of model skill and uncertainty (calibration/validation box in Figure 7). Models that focus on a single stressor often compare predicted to observed data for time series or for grouped years that have contrasting conditions (warm versus cold); then, this information is averaged in some way over the effects of the other stressors [226]. With multiple stressors, a major shift is needed to achieve a multidimensional view of validation to build confidence that the models can capture the dynamics and responses to not only single stressors, but also how the stressors affect each other and how, in various combinations, they affect organisms. The traditional approach will likely suffice for the simulation of the stressors with hydrodynamics-biogeochemical models because the dynamics for testing

occur on relatively fine time scales, so data availability is less of a limitation, especially in well-studied and heavily monitored systems (but see above regarding the complexity of incorporating multiple plankton taxa and their varying nutritional strategies). However, upper trophic level models usually focus on annual predictions (although they can use hourly or daily time steps) so that even extensive long-term monitoring cannot provide observations for all possible combinations (i.e., year types) of the stressors, and additional monitoring will only slowly add more years to the historical record. The accelerating increase in the collection and accessibility of field data [227], the availability of new measurement methods (e.g., [228]), and the sufficient computing power for uncertainty analyses of complex models [229] provide optimism for the future.

In addition to the traditional comparison of predicted versus observed data for model validation, for the upper trophic level models, a bottom-up approach may be used [230]. A bottom-up approach focuses on the estimation and constraining of inputs and parameter values and the testing of the subcomponents of the models. Thus, the importance of the coordination between laboratory experiments and modeling, and among the modeling approaches, is emphasized above. Lorscheid and Meyer [231] offered an approach to model evaluation that they termed "divide and conquer." Their idea was to use designed simulation experiments that evaluate the performance of individual modules and then perform additional simulation experiments that allow assessment of the behavior of the fully coupled system. Other approaches to consider are the use of short-term predictions to provide additional credibility of longer-term forecasts [232], testing *in silico* observed extreme conditions rather than assessing model skill for averaged conditions [233], and validating by assessing the transferability of the models to new locations that, for our purposes here, could have multistressor conditions not observed in the original system of interest [234].

4.5. Challenges in Modeling Climate. While the direct effects of changes in temperature, CO_2, deoxygenation, and other environmental changes are definable with exposure-effect studies, the reality is that many climate changes are occurring with substantial variability at the regional scale. Climate changes are inherently complex and nonlinear, and with changing climate and oceanic conditions, the need to understand nonlinear biological responses and abiotic-biotic feedbacks becomes ever more important. Adding to the challenges of reliably predicting responses by species (from HAB taxa to fish) is the fact that future conditions may fall outside the realm of conditions of the recent past and species may adapt to gradual changes over the long term. Episodic storm events and climate variability affect the timing of freshwater flow, water residence times, the magnitude and timing of nutrient pulses, and the resulting biotic responses (e.g., [42]). Extreme heat and precipitation events have been increasing in recent decades and are projected to increase in frequency and intensity in future decades [1, 235]. A significant increase in the frequency of intense storms and a significant reduction in overall tropical storm frequency are

also predicted [236]. Extratropical winter storms are also likely to change in the future [237]. These dynamics are certainly a challenge for modeling in the context of other stressors. As an example, in September 2018, Hurricane Florence in the Atlantic dropped $\sim 68 \times 10^9$ m^3 of water on the US East Coast, an amount equal to the volume of Chesapeake Bay. Such downpours inevitably wash nutrients (inorganic and organic) off the land, fueling blooms directly or indirectly. The extent to which both lower and upper food webs respond to these extreme events will depend on the timing of the event and the quantity and quality of nutrients discharged from the associated precipitation.

Long-term changes in, or intensification of, natural climate variability, such as monsoons or interannual oscillations, such as those related to ENSO or longer-term cycles, such as the North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO), can also lead to multiple stress conditions for all species. In late 2013 and continuing through much of 2016, anomalously warm water developed in the northeastern Pacific Ocean (e.g., [238, 239]), a feature associated with the unusually strong El Niño event and the PDO. The warm water moved over the continental margin, eventually extending from southern California to Alaska by spring 2015. Coupled with seasonal upwelling, conditions were ideal for the toxic diatom, *Pseudo-nitzschia* spp., which had sufficient nutrients to proliferate, and suitable temperatures for rapid growth. Regulatory limits of the toxic domoic acid were exceeded along the entire coast for months, and toxin impacts were felt at many levels of the food chain, from razor clams and Dungeness crabs to sea lions and whales and porpoises [240]. This was the largest toxic *Pseudo-nitzschia* bloom on the US West Coast thus far and foreshadows the risk of future outbreaks with conditions of increasing temperature and nutrient supply [241].

When applying such models for future regional predictions, downscaling of climate models is necessary. While downscaling is progressing toward finer resolution local predictions [242], the available predictions remain too coarse compared to the needs of the coupled modeling systems for multiple stressors (e.g., [243]), and scenario-based approaches [244, 245] informed by climate models may be more appropriate in the short term. Future projections cannot account for unforeseen events. Interactions of such events are even more difficult to imagine, let alone parameterize. Ensemble models help to overcome some of these difficulties.

4.6. Addressable Illustrative Questions with a Coupled Modeling System. A combined laboratory and coupled modeling strategy (Figure 7) is well suited for evaluating a suite of questions or hypotheses about multistressor interactions and their single and combined effects on organisms. While the specifics of the questions depend on the system of study, the strategy and power of the approach can be illustrated with a set of more generally stated series of questions. We use temperature, deoxygenation, OA, and HABs as representative stressors, although analogous questions can be formulated with other stressors.

The data pool obtained from targeted laboratory experiments merged with existing empirical data can be used to address questions about how stressors affect each other and how individuals respond to exposure. Basic questions include the following: what are the singular and interactive effects of temperature, pCO$_2$, and deoxygenation on HAB growth and toxicity? How do the stressors of temperature, OA, deoxygenation, and HABs interact (beyond their effects alone) to cause growth and mortality effects on the key species at different life stages? Any effort to address these questions must first be explored using laboratory data, which serve as the foundation to support coupled biophysical modeling (hydrodynamics-biogeochemistry). Despite the fact that laboratory data may be vulnerable to experimental artifacts, they provide the best available information to provide numerical thresholds for stressor distributions to be mapped with models in the system of interest. Another fundamental question is: how do the spatiotemporal dynamics of the stressors overlap to create possible "hotspots" of severe effects as well as places of refuge for organisms? Finally, adding habitat, population, and food web modeling enables the expression of the multistressor effects on middle- to upper-level trophic organisms. Model simulations can be designed in a manner using historical conditions and simulation experiments [246] to assess questions such as: how is the habitat suitability for key species (likely by season and subregion such as nursery grounds) affected by stressors singularly and in combination? Under what historical and future conditions will singular and multiple stressors generate linear and nonlinear (not additive) responses for key populations and for food web structure, energetics, and connectivity? What is the role of biotic and indirect effects (e.g., interspecific interactions) in determining the responses to multiple stressors (i.e., habitat versus population versus food web)? These questions and the model simulations used to address them can be further investigated by associating organismal distributions in field surveys (sampling and telemetry) with predicted fields of stressor variables.

All of these questions have management and policy implications. The methods and results must be translated into actionable information that is informative to policy and management [247, 248]. Additional analyses can also address some questions directly relevant to management and policy, such as: what species will likely exhibit the largest responses in productivity and spatial distributions, and how will these cascade into connectivity and food web responses that affect the management of harvest? To what extent can the predicted population and food web responses to multiple stressors under climate change be anticipated from examining historical and the available single and two-way stressor (experimental and modeling) information? Can indicators (early warning) of ecological changes be identified from the simulation of the model projected future stressor conditions combined with the population and food web modeling results? The details of questions and the management issues of the system of interest will enable the specification of testable questions that inform both model development and

subsequent simulation analyses. There is a strong need for such approaches within ecosystem management and forecasting.

5. Summary and Conclusions

The complexity of projecting the effects of the many stressors under which our present and future ocean is experiencing and will experience is extremely challenging. The challenges amplify with increasing consideration of food web complexity. The complexities also amplify with climate variability. Models are advancing and, however imperfect, can be useful for testing the strength of particular factors or variables on outcomes. There remains a pressing need to increase data availability with which models can be parameterized and calibrated, and needs are especially strong for acquiring data outside the norm of single dose-response relationships and to expand consideration of nontraditional food web interactions, including mixotrophy. New modeling approaches, combined with the open-source availability of many models, provide the potential for advancing computational capabilities. Modular, coupled, multitrophic level models provide the flexibility to explore the additive, amplified, propagated, antagonistic, and/or reduced effects that can emerge from the complex direct and indirect interactions of multiple stressors.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Authors' Contributions

WJC conceived the idea of this review. PMG drafted the original manuscript. All other authors contributed to writing and editing.

Acknowledgments

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