

THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

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Breitburg, D.L., J. Salisbury, J.M. Bernhard, W.-J. Cai, S. Dupont, S.C. Doney, K.J. Kroeker, L.A. Levin, W.C. Long, L.M. Milke, S.H. Miller, B. Phelan, U. Passow, B.A. Seibel, A.E. Todgham, and A.M. Tarrant. 2015. And on top of all that... Coping with ocean acidification in the midst of many stressors. *Oceanography* 28(2):48–61, <http://dx.doi.org/10.5670/oceanog.2015.31>.

DOI

<http://dx.doi.org/10.5670/oceanog.2015.31>

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And on Top of All That...

Coping with Ocean Acidification in the Midst of Many Stressors

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“ While ocean acidification has achieved widespread recognition, the consequences of acidification caused by increasing atmospheric CO₂ in conjunction with respiration-driven acidification and changes in temperature, oxygen, productivity, circulation, and other factors has not. ”

ABSTRACT. Oceanic and coastal waters are acidifying due to processes dominated in the open ocean by increasing atmospheric CO₂ and dominated in estuaries and some coastal waters by nutrient-fueled respiration. The patterns and severity of acidification, as well as its effects, are modified by the host of stressors related to human activities that also influence these habitats. Temperature, deoxygenation, and changes in food webs are particularly important co-stressors because they are pervasive, and both their causes and effects are often mechanistically linked to acidification. Development of a theoretical underpinning to multiple stressor research that considers physiological, ecological, and evolutionary perspectives is needed because testing all combinations of stressors and stressor intensities experimentally is impossible. Nevertheless, use of a wide variety of research approaches is a logical and promising strategy for improving understanding of acidification and its effects. Future research that focuses on spatial and temporal patterns of stressor interactions and on identifying mechanisms by which multiple stressors affect individuals, populations, and ecosystems is critical. It is also necessary to incorporate consideration of multiple stressors into management, mitigation, and adaptation to acidification and to increase public and policy recognition of the importance of addressing acidification in the context of the suite of other stressors with which it potentially interacts.

THE CHALLENGE

Acidification is occurring in coastal and ocean ecosystems where human activities are increasingly altering chemical, physical, and biological processes (Doney et al., 2012; Bopp et al., 2013; Duarte et al., 2013). Changing land-based nutrient, sediment, and contaminant inputs, along with fisheries, aquaculture, marine transportation, mining, and energy development at sea, have the potential to alter the severity or effects of acidification on individual organisms and whole ecosystems.

The factors most directly responsible for acidification—increasing CO₂ in Earth’s atmosphere and high rates of respiration fueled by anthropogenic inputs of nutrients to coastal waters—create a cascade of stressors (see Box 1

for definition) that have individual and interactive effects on ocean biota and processes. Increasing atmospheric CO₂ not only acidifies the seawater in which it dissolves, but also leads to increased air and water temperatures that can melt ice, decrease oxygen solubility, and alter patterns of precipitation, wind, stratification, ventilation, and currents (Doney et al., 2012; Levin et al., 2014). Nutrients from land-based activities alter productivity and biomass, which affect the O₂ and CO₂ content of water through respiration and reduced light penetration (Rabalais et al., 2014; Wallace et al., 2014). All of these processes have the potential to change the abundances and distributions of organisms. Given the importance of species interactions,

a major challenge is predicting effects of ocean acidification on species within the context of the communities in which they occur (Gaylord et al., 2014).

As the number of stressors acting on our coastal and oceanic waters increases, the statistical probability of any one stressor affecting a critical physiological or ecological process increases even in the absence of mechanistic interactions among them. Because effects of stressors are often non-additive, the design and interpretation of research incorporating multiple stressors is complex. Whether effects of multiple stressors are additive, greater than additive (synergistic), or less than additive (antagonistic) can depend on the particular response variable (Griffith et al., 2011), level of ecological organization or trophic group studied (Crain et al., 2008), and exposure history. Compensatory mechanisms and pathways within organisms and food webs can influence the magnitude and form of response. Nevertheless, predicting effects of an individual stressor, including acidification, in isolation from the milieu in which it occurs is problematic given the potential for multiple stressors to interact in nonlinear ways (Breitburg and Riedel, 2005; Boyd and Hutchins, 2012; Kroeker et al., 2013; Todgham and Stillman, 2013). In order to develop ecosystem-based management scenarios and approaches that address ocean acidification, it is necessary to understand the sources, interactive effects, and emergent consequences of co-occurring stressors.

Box 1. What is a Stressor?

In this paper, we focus on drivers (environmental and biological variables such as acidity, temperature, hypoxia, and disease) that have been altered by human activities, and refer to these drivers as “stressors” where they have been altered to the extent that the likelihood of eliciting negative responses in physiological or ecological processes is increased. Responses to stressors occur at all levels of biological and ecological organization, and behavioral responses can act as the vehicle to translate effects between physiological and ecological scales.

Understanding and predicting effects of multiple stressors is particularly important, but also most difficult, when effects are non-additive. In such cases, predictions beyond the exact conditions of experiments require a mechanistic understanding that allows for the incorporation of real-world complexity into conceptual and quantitative models.

TEMPERATURE, OXYGEN, AND FOOD WEBS

Of the vast number of stressors that potentially interact with acidification, three—increased temperature, decreased oxygen, and altered food webs—are inextricably linked (Figure 1). They are all consequences of increased CO₂ input into the atmosphere (Doney et al., 2012), and they affect primary production of autotrophs and food quantity and quality for heterotrophs. Input of land-based nutrients and carbonate species can also alter *p*CO₂, *p*O₂, and food supply in receiving waters. All of these stressors are also linked within organisms and food webs through their effects on energy requirements and supply (Pörtner, 2012), and the food web is linked back to environmental O₂ and CO₂ levels through the balance between photosynthesis and respiration. Although the magnitudes of changes in temperature, oxygen, and food will vary with latitude and among habitats, increasing atmospheric CO₂ affects all of these stressors and co-occurs with acidification globally to varying degrees (Figure 1).

Temperature

Increasing atmospheric CO₂ is the major driver of increasing global temperatures (IPCC, 2014). Mean global sea surface temperature is projected to rise by ~2.7°C between the 1990s and the 2090s under the business-as-usual model scenario RCP 8.5 (Bopp et al., 2013). In addition to removing CO₂ from the atmosphere,

the ocean removes a significant amount of the heat that results from greenhouse gas accumulation (Bopp et al., 2013).

A 10°C increase in temperature typically doubles or triples the whole-animal metabolic rate of marine ectotherms. Elevated temperature and *p*CO₂ together can additively elevate or limit the metabolic rate of animals depending on the sensitivity of particular processes (e.g., blood-oxygen transport) and the natural capacity for acid-base regulation (Pörtner et al., 2011). Increased seawater temperatures can increase sensitivity to elevated *p*CO₂ (Kroeker et al., 2013). For example, elevated temperature can exacerbate negative effects of elevated *p*CO₂ on calcification of coralline algae (Martin and Gattuso, 2009) and on aggregation and sinking rates of particles resulting from extracellular transparent exopolymers produced by phytoplankton (Seebah et al., 2014).

Elevated *p*CO₂ has also been suggested to narrow the thermal window of marine heterotrophs and can limit metabolic scope and O₂ carrying capacity (Pörtner et al., 2011). For example, there are studies that show decreased ability for sea urchin larvae to respond to (O'Donnell et al., 2009) or crabs to tolerate (Metzger et al., 2007) thermal stress with elevated *p*CO₂. Active metabolism in the squid *Dosidicus gigas* is reduced at high temperature and elevated *p*CO₂, most likely due to reduced O₂ carrying capacity (Pörtner et al., 2011).

Species interactions can sometimes modify, or be modified by, the effects of co-occurring warming and acidification. For example, mesograzers (amphipods and small gastropods) can reduce the magnitude of the combined effects of these stressors in seagrass communities and mediate their effects on ecosystem properties such as primary production and algal biomass (Alsterberg et al., 2013). Warming and ocean acidification can also influence predator-prey dynamics via altered energy allocation among maintenance, growth, and defense (Kroeker et al., 2014), altered metabolism (O'Donnell et al., 2009), or increased energetic demands in a warmer, more acidic ocean.

Oxygen

Deoxygenation is closely linked to acidification through several mechanisms, highlighting the importance of considering these stressors together. Aerobic respiration, which uses O₂ and releases CO₂, is a major driver of acidification both in metabolically active coastal waters and in deeper, bathyal waters where respiration decreases *p*O₂ and elevates *p*CO₂ over much longer time scales. As a result, dissolved oxygen concentrations and pH are positively correlated in habitats that range from salt marshes and eutrophic estuaries (Cai et al., 2011; Baumann et al., 2015), to oceanic oxygen minimum zones (Paulmier et al., 2011), to kelp forests (Frieder et al., 2012; Figure 2).

As the atmosphere warms, wind-driven upwelling has intensified in some regions (Sydeman et al., 2014). This upwelling causes local shelves to be increasingly bathed by low-pH, low-oxygen waters (Feely et al., 2008). Increased surface layer temperatures are predicted to increase stratification, reducing ventilation and oxygenation of the ocean interior or bottom waters, and increase hypoxia (Keeling et al., 2010). At the same time, increasing temperatures reduce O_2 solubility (although not partial pressure) in seawater. The variety of processes controlling the relationship between pO_2 and pH or pCO_2 results in temporal and spatial patterns that vary in scale and habitat

specificity (Duarte et al., 2013).

The combination of elevated pCO_2 and reduced pO_2 can have strong effects on physiological processes. For example, pH can affect the oxygen-binding ability of blood pigments. Some squid families have very pH-sensitive respiratory proteins and are among the first non-calcifying groups considered to be susceptible to ocean acidification (Seibel, 2015). The combination of elevated pCO_2 and low pO_2 can also decrease the response of invertebrates to bacterial (Mikulski et al., 2000) and protistan pathogens (Boyd and Burnett, 1999) by reducing phagocytosis and the production of reactive oxygen species. Both larval and juvenile

bivalves can be more strongly affected by joint exposure to hypoxia and acidification than to hypoxia alone (Gobler et al., 2014). The effect can vary with age even within life stage, can be non-additive, and may not be predictable from responses to single stressors. In contrast to the above examples, there are also some cases where responses to mild hypoxia can compensate for negative effects of acidification (Mukherjee et al., 2013).

FOOD AND FOOD WEBS

Acidification has a strong potential to alter food web dynamics because both the magnitude and direction of its effects can be species-, trophic mode-, and

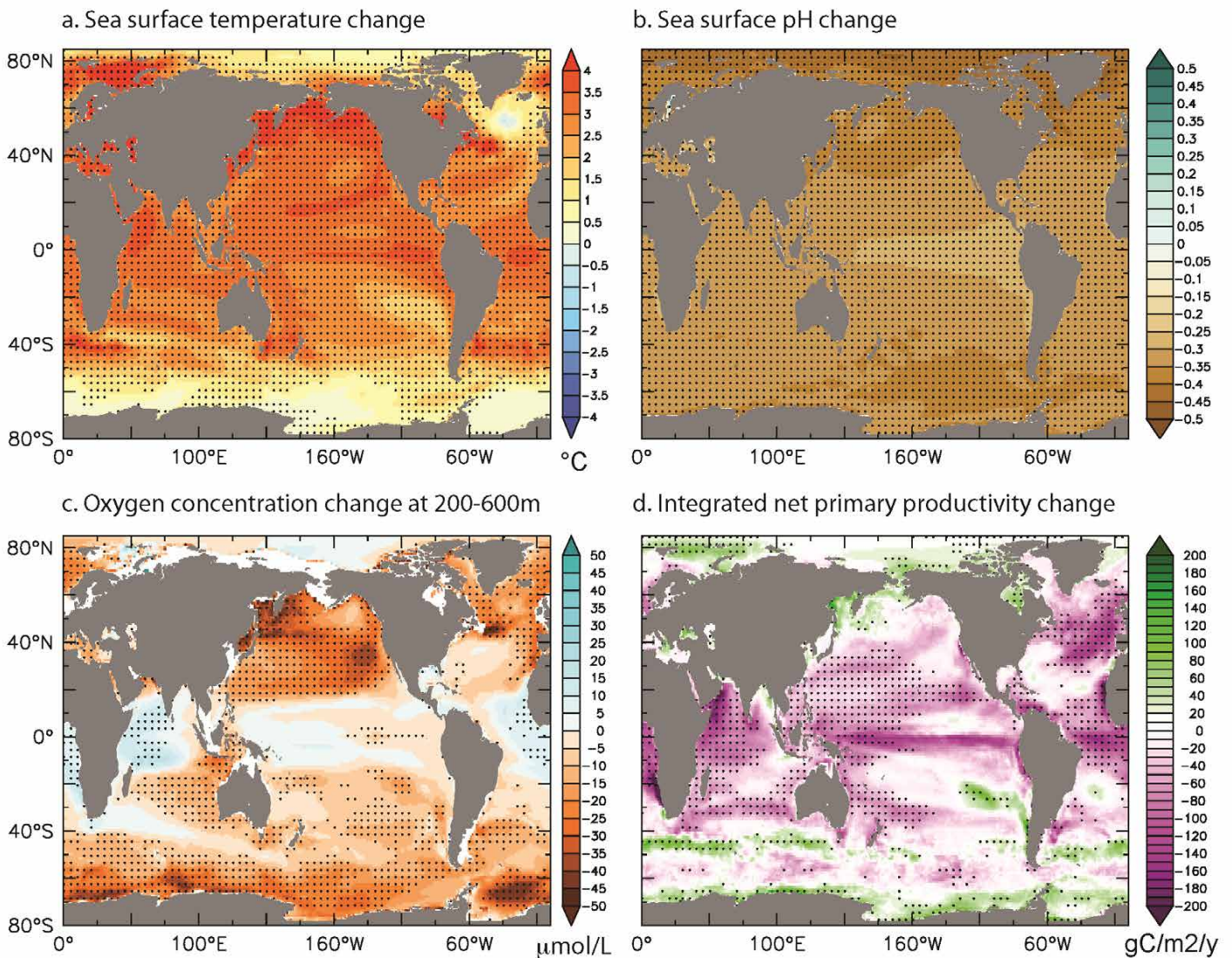


FIGURE 1. Projected changes in sea surface temperature, pH, dissolved oxygen concentration and primary production in 2090–2099 relative to 1990–1999 under the RCP8.5 “business-as-usual” model scenario (Bopp et al., 2013). *Figure courtesy of Laurent Bopp*

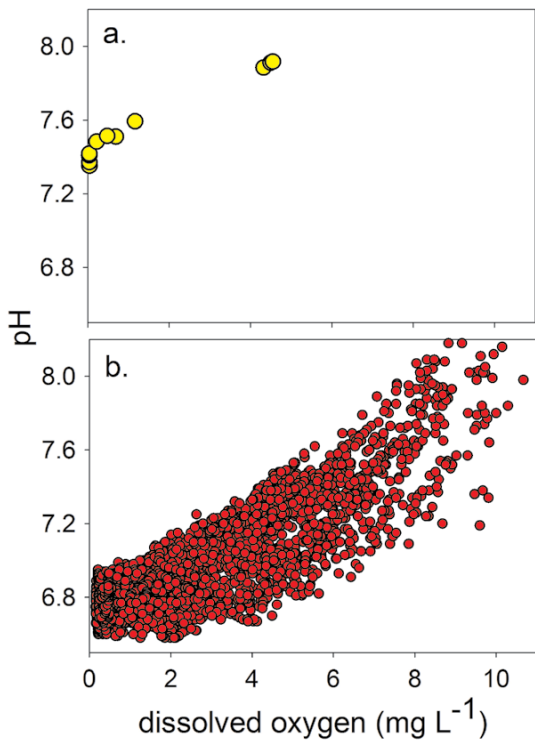


FIGURE 2. Relationship between dissolved oxygen and pH in: (a) a 0 m to 1,000 m depth profile at the Costa Rica Dome (Maas et al., 2011), and (b) in <1 m of water in a salt marsh creek in the Rhode River, MD (author Breitburg's unpublished data).

context-dependent. Increasing $p\text{CO}_2$ can simultaneously stimulate primary production (e.g., Riebesell and Tortell, 2011) and negatively affect consumer physiology (e.g., Stumpp et al., 2013). In addition, the food web is linked back to acidification: photosynthesis fixes carbon and lowers CO_2 concentrations, while respiration increases CO_2 . Changes in food web dynamics may also affect the rate of carbon export from the surface to the benthos and subsequent storage of the carbon in sediment.

Nutrition and responses to increased $p\text{CO}_2$ are intimately linked in autotrophs. Stimulation of primary production by increased $p\text{CO}_2$ can be dependent on sufficient supplies of other nutrients (e.g., Falkenberg et al., 2012), highlighting the importance of the combined effects of increased $p\text{CO}_2$ and anthropogenic nutrient enrichment in coastal waters. Acidification can also exacerbate trace element limitations, for example, by further decreasing iron bioavailability (Sugie et al., 2013). As a result, negative effects of high $p\text{CO}_2$ on phytoplankton can be more pronounced under iron-limited conditions.

Increased $p\text{CO}_2$ alters the food quality

of herbivores by inducing shifts in species composition and succession (Riebesell and Tortell, 2011; Hutchins et al., 2013) as well as toxin concentrations in phytoplankton (Kremp et al., 2012), and by affecting nutrient stoichiometry of organic matter. A decrease in producer quality and palatability has been shown to negatively affect grazers such as copepods (Schoo et al., 2013). Changes such as these near the base of the food web are likely to propagate to higher trophic levels, altering the energy flow and modifying species and community functioning and resilience.

Exposure to elevated $p\text{CO}_2$ is often associated with increased energy costs in consumers (e.g., Stumpp et al., 2012). As a result, acidification may be more likely to have negative effects on consumers under food-limited conditions (e.g., Pedersen et al., 2014). For example, copepods produced fewer eggs under experimentally elevated $p\text{CO}_2$ when food was limited but not under *ad libitum* feeding (Thomsen et al., 2013; Pedersen et al., 2014). In the field, high food availability can outweigh ocean acidification effects, sometimes allowing calcifying heterotrophs to thrive in high $p\text{CO}_2$ environments such

as the Kiel fjord (Thomsen et al., 2013). However, food limitation does not always exacerbate acidification effects. In experiments on Antarctic pteropods, ocean acidification led to metabolic suppression under high food conditions but not when food was limiting (Seibel et al., 2012).

Food acquisition and digestive processes are also sensitive to ocean acidification (e.g., Stumpp et al., 2013) as well as to other stressors. Sea urchin larvae exposed to elevated $p\text{CO}_2$ suffered from a drop of gastric pH, which directly translated into decreased digestive efficiencies and triggered compensatory feeding (Stumpp et al., 2013). In experiments on other species, ocean acidification reduced feeding efficiency (Vargas et al., 2013), attenuated the induced defenses of prey (Bibby et al., 2007), and reduced foraging performance of predators (Ferrari et al., 2011).

Like acidification, some co-occurring stressors (e.g., elevated temperatures) directly influence both primary producers and consumers with high variability in the magnitude and direction of effects. Other stressors (e.g., nutrient enrichment, fishing) directly target particular trophic levels and affect others only indirectly through altered production or consumption rates. The variability of effects of individual stressors on trophic interactions and food web structure, and the wide range of ways that altered food webs can modify stressor effects, are likely to translate into highly variable impacts in space and time.

MULTIPLE DRIVERS AND MODIFIERS OF ACIDIFICATION

Environmental factors that modify patterns of acidification can also exert physiological stress through independent mechanisms, including osmotic stress associated with freshwater input, thermal stress associated with greenhouse effects of increasing atmospheric CO_2 , and increased biomass and hypoxia associated with anthropogenic nutrient loading and intensified upwelling. These potent modifiers of acidification combine to create patterns of temporal, spatial, and

habitat-specific variation in the severity of acidification (Table 1, Figures 3 and 4).

For example, the severity of atmospheric CO₂-driven acidification varies spatially due to the effects of temperature on CO₂ solubility and the relationship between salinity and alkalinity. CO₂ is released during remineralization of organic carbon, as water circulates throughout the ocean over the course of centuries and through coastal systems over much shorter time scales. High-CO₂ water is brought to the surface via upwelling over multiple spatial and temporal scales. Due to greater nutrient availability, upwelling and coastal regions generally support high primary productivity, which results in enhanced uptake of atmospheric CO₂ and eventual export of CO₂ below the pycnocline due to sinking and respiration. Daily and seasonal cycles associated with changes in temperature, photosynthesis, circulation, tides, and ice cover also drive cycles in carbonate chemistry.

Co-occurrence of acidification with other stressors also varies (Figures 1 and 4). Like acidification, warming and

deoxygenation are occurring globally, with their magnitudes varying geographically (Bopp et al., 2013). In addition to obvious daily and seasonal cycles, temperature fluctuates both on shorter and longer time scales as a result of different physical processes such as internal waves and the North Atlantic and Pacific Decadal Oscillations. The intensities of coastal stressors are modulated by anthropogenic activities, freshwater input, and the composition of terrestrial soil and vegetation (Duarte et al., 2013). The following examples from polar waters, coral reefs, and estuaries illustrate the variety of drivers that affect the patterns and severity of acidification and some of the range of important co-occurring stressors.

Polar Environments

Calcium carbonate saturation states in polar surface waters are already relatively low (Steinacher et al., 2009) due primarily to the enhanced solubility of CO₂ in cold water. These systems are therefore particularly sensitive to factors that further increase pCO₂. The most intensive

warming caused by increasing atmospheric CO₂ is occurring at the poles, resulting in reduced ice cover, especially in the Arctic. Reduced sea ice cover can result in increased air-sea exchange and increased primary productivity, leading to greater uptake of atmospheric CO₂. Although rising temperatures reduce CO₂ solubility somewhat, this enhanced CO₂ uptake, combined with decreased alkalinity due to freshwater input from ice melt, has already created aragonite undersaturation in surface waters of the Canada Basin (Yamamoto-Kawai et al., 2011) and western Arctic Ocean (Robbins et al., 2013). Because polar animals often have narrow temperature tolerances and low capacity for thermal acclimation (Somero, 2012), intense warming near the poles may cause physiological stress, range contractions, and migration into deeper waters. Warming has also allowed some temperate species to move poleward, leading to altered competitive interactions (Ingels et al., 2012). Reduced carbonate saturations states and increased acidity may, however, create barriers to some poleward migrations.

TABLE 1. Overview of the multiple causes of acidification, along with examples of impacted habitats and predominant co-occurring stressors.

Drivers of Acidification	Particularly Impacted Habitats	Co-stressors and Coupled Processes
Atmospheric CO ₂	Worldwide but spatially variable (polar waters are particularly acidic because CO ₂ is more soluble in cold water)	Warming strongly affects polar and coral reef organisms and melts sea ice, increasing air-sea exchange of CO ₂ . Warming also increases stratification and reduces ventilation of the ocean interior, leading to oxygen decline and changes in primary productivity due to subsequent changes in nutrient ratios.
Respiration/eutrophication	Estuaries, sediment-based benthos, deep waters	Hypoxia, eutrophication. Effects may be mitigated, at least during daylight hours, by increased primary productivity in shallow waters, but exacerbated in deepwater habitats that receive marine snow where particles sink and decay.
Upwelling	Coastal environments, equatorial regions	Warming can cause changes in upwelling winds. Nutrient-rich upwelled water can exhibit reduced oxygen levels due to respiration, but it is also cooler, which can provide relief from thermal stress (e.g., reefs).
Atmospheric deposition of nitrogen and sulfur from combustion and agricultural activities	Coastal environments	pH can increase or decrease, depending on type of deposition.
Ice melt	Polar environments	Can lead to altered stratification, light and nutrient availability, freshwater input, and increased atmospheric exchange. Freshwater input tends to decrease salinity and alkalinity, reducing the buffering capacity of seawater.
Altered terrestrial hydrological and geochemical cycles	Estuaries and coastal environments	Altered alkalinity, alkalinity:DIC ratio, salinity, stratification, eutrophication, sedimentation, and terrestrial pollutants. Direction of change will depend on changes in the magnitude, form and timing of precipitation.
Precipitation and storms	Coral reefs and other shallow environments	Reduced salinity and alkalinity. Extreme storms may increase in frequency, and damage to reefs may be intensified if acidification weakens reef structures. Wind associated with storms mixes and oxygenates hypoxic waters, but precipitation increases stratification.

Shallow-Water Coral Reefs

Acidification is of particular concern for reefs because reef structures are built from the calcareous skeletons of corals and coralline algae. Carbonate chemistry varies on reefs as a result of calcification, photosynthesis, and respiration, as well as wave energy and morphology (Falter et al., 2013). Physiological stress associated with elevated temperatures can result in expulsion of symbiotic algae from coral tissues, a global phenomenon known as “bleaching” (Baker et al., 2008). Upwelling of cool, nutrient-rich water can provide relief from warming (e.g., in the eastern Pacific), but upwelled water is also more acidic and lower in oxygen. Upwelled nutrients, along with epizootics and fisheries removals that reduce herbivore populations, can alter the ecological balance between benthic algae and corals. Climatological warming may lead to increased frequencies of very strong tropical cyclones (Knutson et al., 2010). The damage to reef structures and reduction in coral cover from these storms may be compounded if acidification leads to weakened reef structures (Manzello et al., 2008).

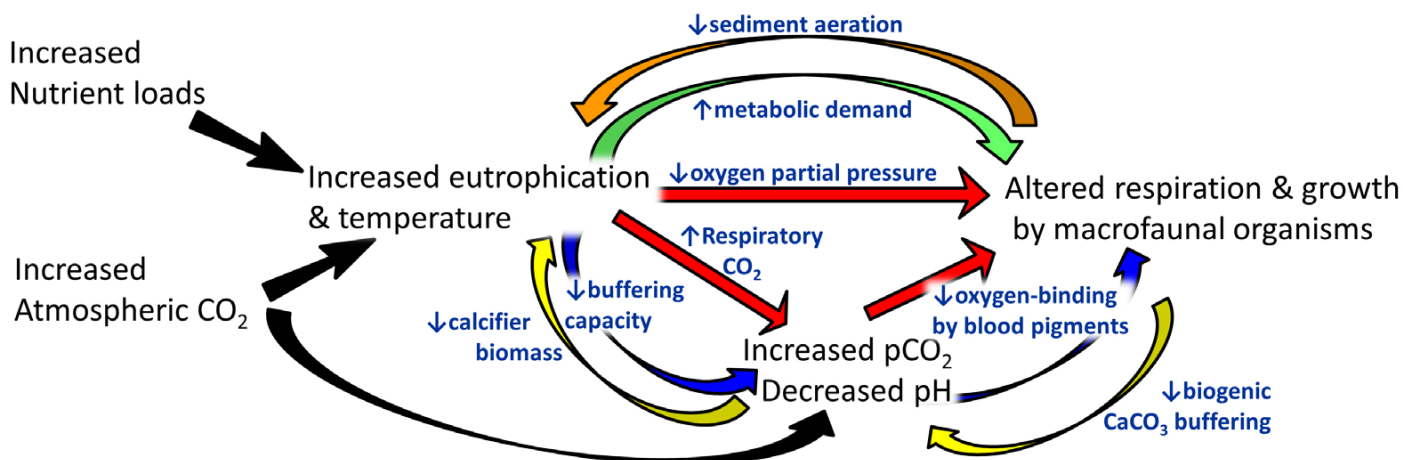
Estuaries

Proximity to dense centers of human population and traditional uses of estuarine waters for fisheries, shipping, and disposal of human waste expose estuaries to many factors that can affect acidity and act as co-stressors with acidification. Estuarine carbonate chemistry is modified by freshwater inputs, atmospheric deposition, nutrient stimulation of biomass and production, and upwelling, and many estuaries experience natural cycles of acidity and oxygen concentrations driven by respiration, photosynthesis, and tides. Freshwater input from rivers increases buoyancy and therefore stratification, which can stimulate primary productivity but it also tends to decouple photosynthesis from respiration (Salisbury et al., 2008). The salinity gradients created by the mixing of fresh and saline waters create spatial variation in acidification, and salinity itself acts as a co-stressor for many estuarine organisms. Nutrient loading from both terrestrial runoff and atmospheric inputs of sulfur and nitrogen can stimulate primary production and trigger a cascade of effects, including decreased

light penetration, reduced benthic primary production, altered species composition, and intensified respiration leading to hypoxia (Cloern and Jassby, 2012) and acidification.

Within estuaries, about a quarter of the organic inputs are respired by sediments (Hopkinson and Smith, 2005). Most of this respiration is confined to the upper millimeters to centimeters of sediment (Glud, 2008), elevating $p\text{CO}_2$ (and decreasing pH and Ω) within a horizon critical to bivalve development (Green et al., 2009). Sharp pH and $p\text{CO}_2$ changes at narrow depths within the sediment pose serious challenges to benthic organisms (Cai and Reimers, 1993). The demise of oyster reefs resulting from overfishing, disease, and poor water quality also results in the loss of CaCO_3 shells and their potential to increase alkalinity (and, therefore, the buffering capacity) of near-bottom waters (Waldbusser et al., 2013).

Respiratory CO_2 currently has a greater effect on acidification than atmospheric CO_2 in many estuaries. However, the latter will exceed the former in many systems near the end of the twenty-first century (Feely et al., 2010; Cai et al.,



Increased oxygen consumption with increasing temperature	Melting sea ice, increased precipitation	Increased microbial respiration and water column stratification	Decreased calcification and filtration by bivalves and corals	Reduced benthic biomass
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FIGURE 3. A wide range of anthropogenic stressors—some related to increasing atmospheric CO_2 , and some caused by other human activities—can modify both the effects and severity of acidification through a variety of pathways. Effects of acidification can be modified when other stressors directly affect target species or processes (green arrow) alter the patterns or severity of acidification (blue), or influence targets through both of these pathways (red). Acidification can also modulate the effects of other stressors (yellow) and target species and ecological processes that can alter the severity of patterns of acidification (orange). Each effect may then indirectly influence target species and processes through any of the connecting pathways. Examples are shown in arrow labels and colored boxes that match arrow colors.

2011), and their interactive effect will also increase with time (Cai et al., 2011). Combined effects of atmospheric CO₂ and respiration on estuarine pCO₂ and pH will depend on a number of system- and location-specific factors, including algal bloom dynamics, alkalinity, stratification, and freshwater residence time. But if current eutrophication is not reduced and atmospheric CO₂ rises to 800 ppm, even the strongly buffered bottom waters of the northern Gulf of Mexico will become undersaturated for aragonite, with pH_{total} declining from a pre-industrial pH value of 8.19 to 7.34 (Cai et al., 2011).

WHEN ARE MULTIPLE STRESSORS IMPORTANT? PARALLELS IN PHYSIOLOGICAL AND ECOLOGICAL PERSPECTIVES

A theoretical framework for predicting the effects of multiple stressors is needed because it is impossible to experimentally test all combinations of stressors on all organisms and ecological processes of interest. Although approaches and endpoints differ, physiologists and ecologists tend to agree on some of the features that are important to consider in understanding when and where multiple stressors will cause large, threshold, or non-additive effects.

Modes of Action¹

Cellular responses to a stressor that decreases the physiological capacity to compensate or respond to a second stressor result in greater than additive stressor effects (Chen and Stillman, 2012). Responding to several stressors simultaneously can involve multiple molecular and cellular signaling pathways (i.e., modes of action) and can result in considerable energy expenditures. Even if the way in which stressors act on an organism is similar, the extra energy expenditure required to cope with multiple challenges can reduce an organism's resilience to additional challenges (Melzner et al.,

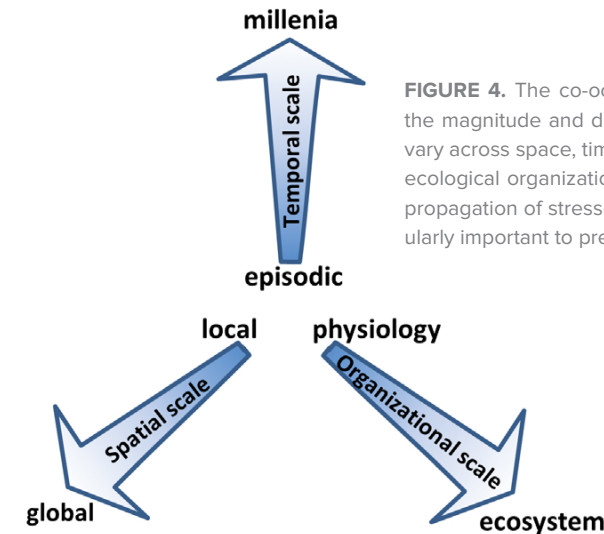


FIGURE 4. The co-occurrence of stressors, as well as the magnitude and direction of their combined effects, vary across space, time, and the levels of biological and ecological organization. Mechanisms that influence the propagation of stressor effects across scales are particularly important to predicting multiple stressor effects.

2013). In contrast, stressors that elicit similar response pathways without additional energy expenditure, and stressors with differing modes of action but that induce a pathway that is protective against a range of stressors, can result in effects that are less than additive or less severe (Sinclair et al., 2013).

A concept analogous to modes of action is used by ecologists to examine whether multiple stressors tend to affect the same species or processes within an ecosystem (rather than the same physiological pathway within an individual), and whether different species or processes tend to be susceptible to different stressors (negative co-tolerances; Vinebrooke et al., 2004; Crain et al., 2008). Multiple stressors tend to elicit the largest ecological effects when different species—especially species with similar ecological roles—are sensitive to different stressors, and when effects of one stressor reduce the ability of the system to respond to additional stressors. The ecological analog of inducing “protective” pathways may also be important. In some cases, once stressors cause an ecosystem to become degraded or dominated by hardy, stress-tolerant species, the new ecosystem state may actually be more resilient to additional stressors (Côté and Darling, 2010).

Severity

Whether the response to multiple stressors is additive can also depend on the unique combination of values (e.g., severity, concentration) involved. Decreased pH can lead to positive, neutral, or negative effects depending on the tested temperature (Gianguzza et al., 2013; Sett et al., 2014; Kroeker et al., 2014). The relationships among the typically nonlinear dose-response curves of each stressor with the various environmental factors that characterize a species’ (or population’s) environmental niche create variation in both the magnitude and additivity of responses to multiple stressors. Severity is important to consider when scaling up from physiological to food web or ecosystem responses because severity can determine whether the responses of interacting species include altered behavior, reduced growth and reproduction, or mortality. Each of these effects will have different consequences for species interactions and will vary in their potential to be exacerbated by additional stressors. Stressors that reduce population size may be particularly important; by reducing populations, they may reduce genetic variability and thus reduce a population’s evolutionary capacity for adaptation (Munday et al., 2013).

¹A mode of action is an integrated, coordinated molecular, cellular, and physiological response to a stimulus or change in environmental condition(s).

Persistent and Sequential Effects

Exposure to stressors during one part of an animal's life can have lasting impacts on its performance later in life (Podolsky and Moran, 2006) or on its offspring. The energetic costs of responding to multiple stressors may persist (carry-over effects) or only start to manifest in the previously exposed organism after it has been removed from these condi-

increase energy demand.

Sequentially applied stressors may be particularly important when one stressor increases the sensitivity of an organism to subsequent stressors. For example, exposure of red king crab embryos to low pH reduces subsequent survival of larvae under low food conditions (Long et al., 2013). Individuals coping with persistent stress (e.g., lower pH) could be more sus-

“Improved literacy in the field of multi-stressor interactions can help to focus attention on the problem and create the political will to find solutions that keep our ocean healthy for future generations.”

tions (latent effects). Offspring may also be affected by parental exposure (transgenerational effects). Exposure to stressors can have long-term consequences that are not fully captured through short-term observations. Previous studies have demonstrated that exposure of oyster larvae to elevated $p\text{CO}_2$ can result in carry-over effects on the growth rate of juveniles (Hettinger et al., 2012) and that exposure of urchin adults to elevated $p\text{CO}_2$ can cause latent transgenerational effects on juvenile survival that are not apparent in larvae (Dupont et al., 2013). Transgenerational effects of exposure to elevated $p\text{CO}_2$ have been noted for both Atlantic silversides (Murray et al., 2014) and three-spined stickleback (Schade et al., 2014) fishes. Increased energy demand associated with elevated $p\text{CO}_2$ (e.g., in fishes; Rummer et al., 2013) may result in less energy being allocated to processes that are important for long-term aerobic fitness or in there being less energy available for later developmental stages. These persistent effects may be amplified by exposure to additional stressors that also

ceptible to additional stressors such as heat waves or pulses of freshwater from intense storms than if they were living under more benign conditions (Miller et al., 2014). Species with complex life cycles may be more susceptible to multiple stressors because life-cycle completion can be disrupted by stressors in one of several habitats (Crozier et al., 2008).

At higher levels of organization, effects can persist if a stressor influences a slow ecological process or influences a species or process that is part of a “return trajectory” that would otherwise allow a system to recover along the same path as it was perturbed (Scheffer and Carpenter, 2003). This results in a situation similar to a carry-over effect in an organism, where the system is changed due to previous exposure to one or more stressors. Because of lags or lack of recovery from initial stressors, the order and timing of exposure to multiple stressors can strongly influence outcomes. In contrast, resistance to subsequent stressors can be enabled when the initial stressors result in a community dominated by stress-resistant species. Degraded coral

reefs that are composed of disturbance-tolerant massive corals are more tolerant of thermal stress than more pristine reefs composed of both sensitive and tolerant species (Darling et al., 2010).

Number and Pattern of Stressors

The number and pattern of stressors may be especially important in creating large or threshold changes. As the number of stressors increases, the probability that the mix will include stressors with different modes of action also increases. At the level of the individual or clone, an increase in the number of stressors with different modes of action could increase the likelihood of exceeding physiological plasticity. At the level of the food web, the likelihood of affecting different species and reducing functional redundancy and compensatory pathways may increase (Vinebrooke et al., 2004). As the number of stressors increases, the statistical likelihood that a slow ecological process or a species or process that is part of a return trajectory will be affected also increases. As a result, the likelihood of persistent and threshold responses may increase. Meta-analyses indicate that the probability of greater than additive effects increases if more than two stressors are present (Crain et al., 2008).

Spatial and temporal patterns of stressor exposure are also particularly important when considering multiple-stressor effects, whether at the physiological or ecological level of organization. Spatial and temporal patterns determine the co-occurrence of stressors, their coincidence with sensitive life states, the sequence of exposures, and ultimately the cumulative stress impacts.

THE IMPORTANCE OF MULTIPLE RESEARCH APPROACHES TO MULTIPLE STRESSOR QUESTIONS

No single research approach can achieve all goals or provide a comprehensive understanding of the many factors that affect acidification as well as its effect on organisms. Instead, diverse approaches

are needed (Table 2). The goal of any suite of approaches should be to generate and utilize physiological and ecological mechanistic understandings that will facilitate prediction. Information on the patterns of co-occurrence of acidification and other stressors in the field can provide important guidance on the design of experiments. Consideration of temporal and spatial scales is important both to the design of studies and the interpretation of results.

Laboratory incubations used to test individual species in controlled, single or multiple stressor experimental conditions have brought significant insight into mechanisms that can provide predictive power. Mesocosms are often large enough to include multiple trophic levels, natural light and temperature regimes, benthic-pelagic interactions, and other processes of interest. They also permit manipulations of the pelagic environment (Riebesell et al., 2012) and measurement of larger-scale natural processes like aggregation and particle sinking. Natural gradient experiments take advantage of the fact that the ocean is replete

with strong natural gradients in hydrographic parameters that can act as stressors and that manifest in space or time. These gradients may offer valuable clues about how natural systems may respond to multiple stressors on different scales, including over evolutionary time. In both manipulative experiments and studies of natural populations, high-throughput molecular approaches will likely provide new insight into effects of multiple stressors on populations and communities (genomics and metagenomics) as well as mechanisms and pathways through which stressors combine to affect organisms (transcriptomics, proteomics, and metabolomics). Studies of the fossil and geochemical records, geochemical proxies (Levin et al., 2015, in this issue), models, and meta-analyses have the potential to provide a more synthetic view of multiple stressor consequences. The general strengths and weaknesses of these approaches are not unique to multiple stressor acidification research, but the urgency and complexity of the problem argue for the need to use all available tools.

RESEARCH PRIORITIES

Several areas and approaches for future research are clearly necessary to improve our understanding and ability to predict the complex dynamics of systems challenged by multiple stressors that include ocean acidification.

1. We must better characterize the spatial and temporal patterns of potentially interacting stressors occurring in natural systems. This includes creating and enhancing observing systems in a variety of pelagic, benthic, and shallow-water habitats in estuaries, coastal waters, and the open ocean. We need to identify and understand the occurrence and variability of components that are physical, chemical, and biological in nature. With a better characterization of natural systems, it will be possible to design experiments that reveal mechanisms behind the biological responses (from physiological to ecosystem scales) to multiple stressors most relevant to current conditions and future scenarios.

TABLE 2. Research approaches to predict effects of multiple stressors on effects of acidification. The list is not intended to be exhaustive.

Research Approach	Advantages	Disadvantages	Example of Use to Examine Multiple Stressors that Include Acidification
Laboratory incubations	Can test specific mechanisms	<ul style="list-style-type: none"> • Most simplified conditions relative to natural exposures 	Temperature and $p\text{CO}_2$ effects on crucial oxygen partial pressure (Seibel, 2011)
Mesocosms and FOCE (free ocean CO_2 enrichment) experiments	Can often include more natural variation and complexity in physical environment and ecological interactions	<ul style="list-style-type: none"> • Can be difficult to disentangle the contribution of specific processes to net responses within mesocosms harboring a complex community • Expense limits replication and number of treatments to parse out individual and interactive effects of several stressors 	Presence of grazers eliminated beneficial effects of increased $p\text{CO}_2$ and warming on benthic microalgae (Alsterberg et al., 2013)
Natural gradient experiments and field sampling	Possible to use natural gradients, including outplant and transplant experiments, to better understand the relative contributions of covarying factors	<ul style="list-style-type: none"> • Difficult or impossible to control for co-varying factors • Gene flow from non-affected populations may limit conclusions about potential evolutionary responses 	Mussels grew more at higher $p\text{CO}_2$ site with higher particulate organic carbon (POC) and particulate organic nitrogen (PON) than at lower $p\text{CO}_2$ site with lower POC and PON (Thomsen et al., 2013)
Fossil record and geochemical signatures	Provides insight into historical consequences of processes of interest	<ul style="list-style-type: none"> • Possibility of extinct organisms irrelevant to extant communities • Inability to confidently know all environmental parameters during time period of interest 	Acidification and hypoxia during the Eocene Thermal Maximum 2 and the Paleocene Eocene Thermal Maximum (Foster et al., 2013)
Modeling and meta-analysis	Can synthesize results of diverse sources and approaches in a predictive construct	<ul style="list-style-type: none"> • Dependent on other approaches to generate input data and mechanisms • Difficult to incorporate full range of natural complexity 	Acidification worsened hypoxia by reducing mineral ballast fluxes (Hofmann and Schellnhuber, 2009)

2. As the number of potential stressors is almost limitless, it is important to identify those stressors most likely to interact with acidification, causing effects at a level likely to substantially alter the system. Environmental conditions that might be innocuous on their own may show debilitating impacts to the system when combined with elevated $p\text{CO}_2$, or may exert a mitigating effect with elevated $p\text{CO}_2$. Variability must be considered: for example, fluctuating conditions and static conditions differ in stimulating resilience and negative responses.

3. Approaches that lead to a better understanding of stressor effects across a range of intensities and temporal and spatial scales should be emphasized. This includes studies that assess responses to a gradient of stressors and examine tipping points that might also be present. It will also be necessary to understand responses to long-term exposure, including both adaptive and evolutionary responses. Understanding mechanisms driving these responses on cellular, organismal, or ecosystem levels will result in data more useful for model projections and upscaling.

4. Additional mechanistic research focusing on specific levels of organization is still required to build predictive models; finding underlying mechanisms that are general across species and processes is important. When examining these mechanisms, it is essential to consider nuances that might have particular beneficial or negative influences on different organisms. In addition, understanding how acidification alters food webs in conjunction with other stressors will be critical to predicting effects in nature.

5. Predictive models are needed to advance the understanding of multiple stressor effects. Once created, predictive models should be validated with mesocosm and field experiments, and at least some should be run on extended timeframes to allow for the incorporation of

individual and generational adaptation to multiple stressors. While looking to the future, we can also look to the past for guidance. Examining the geological record and making use of geochemical proxies (Levin et al., 2015, in this issue) allows us to test effects at more complex natural ecological scales and to include natural variability.

6. It is necessary to recognize that all of these stressors, interactions, and mechanisms have the potential to change over different habitats and seasons. By integrating observing systems, stressor identification, mechanistic approaches to identifying impacts, mesocosm/field studies, and model development, it is possible both to make unanticipated discoveries and to improve our predictive capacity for identifying the impacts of multiple stressors across marine environments.

MANAGING FOR MULTIPLE STRESSORS

The biological and ecological effects of ocean acidification and other stressors have the potential to substantially degrade many of the marine ecosystem services upon which human communities around the world depend (e.g., Cooley et al., 2009; Doney et al., 2012). Ocean management approaches to reducing the negative impacts of ocean acidification have been proposed for coastal and coral reef systems (Strong et al., 2014) and have been developed at the regional planning level (Washington State Blue Ribbon Panel on Ocean Acidification, 2012). Similar to other global-scale environmental problems, management approaches can be roughly divided into (1) mitigation options that aim to limit the underlying drivers of acidification and other stressors, and (2) adaptation options that aim to minimize the negative impacts of these stressors on natural and managed ecosystems and human communities.

A key to managing multiple stressors is to identify underlying commonalities in solutions to address more than one ocean stressor simultaneously, thus maximizing

net benefits from action. Ocean management options must be assessed in terms of effectiveness, cost, scalability, and direct and indirect environmental consequences. In many cases, trade-offs will arise because solutions that may maintain or maximize some ecosystem services potentially may also have negative effects or trade-offs for other ocean uses (Ruckelshaus et al., 2013). Some of the proposed solutions to ocean acidification are similar to those needed to address long-standing environmental problems such as high nutrient loads to estuarine and coastal waters. Often problems arise because of conflicting economic interests and values of distinct stakeholder groups. Therefore, managing ocean acidification and co-occurring stressors requires substantial efforts to improve science-policy coordination, raise public awareness, establish (or adapt existing) legal and regulatory frameworks, develop better governance, and address and reduce political barriers to action (e.g., Kelly et al., 2011).

Mitigation of estuarine and coastal acidification, hypoxia, and poor water quality are linked via the need to reduce land-based sources of pollution (e.g., excess nutrients, erosion of soil organic matter, nitrogen and sulfur emissions to the atmosphere). Options have also been proposed for remediating coastal waters by, for example, restoration efforts that would enhance algal and seagrass carbon uptake and in turn reduce eutrophication, hypoxia, and acidification. Some proposed CO_2 removal methods involve making seawater more alkaline, which could potentially also address acidification directly on some scale, though none of these approaches has moved beyond either design studies or small-scale pilot investigations.

Adaptation strategies focus on strengthening the resilience of ecosystems and human systems in the face of ongoing, and perhaps rising, stressor levels such that these systems maintain key functions and delivery of essential benefits and services. Proposed adaptation efforts for acidification include reducing

local stressors such as overfishing, erosion, and pollution, and incorporating global-scale ecological pressures in regional marine spatial planning frameworks. Enhanced flexibility is required in spatial planning and resource management, which is also typically place- and time-based, to address the already ongoing shifts in the geographic ranges of marine populations, community composition, and fishery harvests in response to multiple stressors. Growing evidence of differential susceptibility and acclimation of organisms, subpopulations, and communities to acidification and other stressors can be incorporated into management by targeting local refugia for special protection or by adapting aquaculture practices. Overlying all of these efforts is the need for improved and coordinated monitoring networks of the coupled natural-human system.

CONCLUSIONS

There is a strong need to raise awareness globally that CO₂ accumulation in the atmosphere is changing multiple aspects of the ocean environment, potentially with major negative consequences. These ocean changes are the true face of climate change. While ocean acidification is widely recognized, the consequences of acidification caused by increasing atmospheric CO₂ in conjunction with respiration-driven acidification and changes in temperature, oxygen, productivity, circulation, and other factors is not. A major effort that communicates this important point is needed that targets all stakeholders—the public, regulators, policymakers, industry, and other scientists. Improved literacy in the field of multi-stressor interactions can help to focus attention on the problem and create the political will to find solutions that keep our ocean healthy for future generations. ☐

ACKNOWLEDGEMENTS. We would like to thank the organizers of the 2013 Ocean Acidification principal investigators meeting for bringing the authors together to focus on this important issue, and S.R. Cooley and the other editors of this volume for their help and support throughout the writing

process. A. Maas provided data plotted in Figure 2a. DLB thanks K. Cottingham for sharing ideas on multiple stressors, and I. Fang and H. Soulen for collecting data plotted in Fig. 2b. Funding for research on acidification and multiple stressors was provided by NOAA-CSCOR NA10NOS4780138 to DLB, NASA NNX14AL8 to JS, NSF OCE-1219948 to JMB, NSF OCE-927445 and OCE-1041062 to LAL, NSF EF-1041070 to W-JC, a Linnaeus grant from the Swedish Research Councils VR and Formas to SD, NSF EF-0424599 to SCD, NSF OCE-1041038 to UP, NSF EF-1316113 to BAS, NSF ANT-1142122 to AET, NSF OCE-1316040 to AMT, and the NOAA Ocean Acidification Program Office to BP, LMM, and WCL. The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA.

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