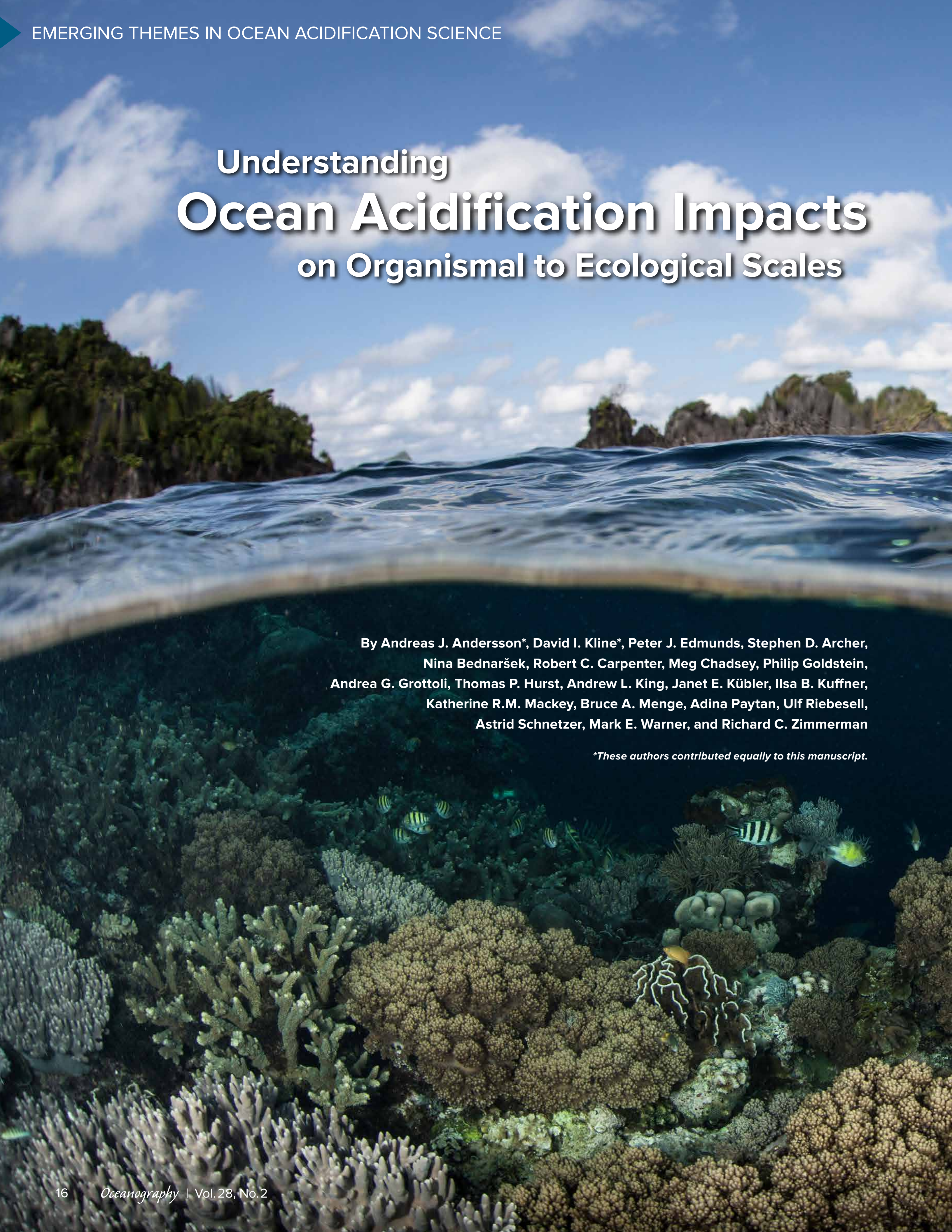
THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

DOI

http://dx.doi.org/10.5670/oceanog.2015.27



Understanding Ocean Acidification Impacts on Organismal to Ecological Scales

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ABSTRACT. Ocean acidification (OA) research seeks to understand how marine ecosystems and global elemental cycles will respond to changes in seawater carbonate chemistry in combination with other environmental perturbations such as warming, eutrophication, and deoxygenation. Here, we discuss the effectiveness and limitations of current research approaches used to address this goal. A diverse combination of approaches is essential to decipher the consequences of OA to marine organisms, communities, and ecosystems. Consequently, the benefits and limitations of each approach must be considered carefully. Major research challenges involve experimentally addressing the effects of OA in the context of large natural variability in seawater carbonate system parameters and other interactive variables, integrating the results from different research approaches, and scaling results across different temporal and spatial scales.

BACKGROUND: THE CHALLENGE

Since the beginning of the Industrial Revolution, oceanic absorption of carbon dioxide (CO_2) originating from human activity has increased surface seawater acidity (as measured by the increase in hydrogen ion concentration) by about 26% (Doney et al., 2009). This ocean acidification (OA), which has been well documented at multiple open ocean locations globally (Bates et al., 2014), is highly predictable from fundamental knowledge of the carbonate chemistry of seawater that controls pH. If CO_2 emissions continue to increase at the present rate, model projections suggest that surface seawater acidity will increase by an additional 100–150% by the end of this century (Joos et al., 2011; Orr et al., 2005). There is no precedent for this rate of change in seawater acid-base chemistry in the entire geological record (Hönisch et al., 2012).

The projected changes in seawater pH and speciation of dissolved inorganic carbon (DIC) portend significant consequences for individual marine organisms, communities, ecosystems, food webs, and dependent human populations (Doney et al., 2009; Kroeker et al., 2013; Barton et al., 2015, in this issue). Yet, many questions about the effects on biological systems, including the timing, scale, and magnitude of the impacts, remain unanswered. A better understanding is essential for taking action to manage the inevitable ecological and socioeconomic consequences of OA.

Our initial understanding of the effects of OA on marine organisms was based on small-scale, short-term laboratory experiments with single species. These early studies on mainly calcifying organisms suggested negative effects on growth, calcification rate, and survival (e.g., Smith and Roth, 1979; Smith and Buddemeier, 1992; Marubini and Atkinson, 1999). Over the past decade, numerous investigations using a range of approaches both in the laboratory and in natural environments at different scales and durations have mostly confirmed these initial findings, but they have also highlighted that the responses are more nuanced and variable than indicated by early experiments (e.g., Ries et al., 2009; McCulloch et al., 2012). For example, elevated seawater CO_2 stimulates the productivity of some marine algae and seagrasses as well as elevating nitrogen fixation by cyanobacteria (Durako, 1993; Zimmerman et al., 1995; Beer and Koch, 1996; Kübler et al., 1999; Gordillo et al., 2001, Invers et al., 2001; Hutchins et al., 2007; Mackey et al., 2015, in this issue). Additionally, most OA studies are unable to account for the potential for organisms to adapt and/or physiologically acclimatize to OA conditions and the potential trade-offs involved (Kelly and Hofmann, 2013; Collins et al., 2014; Sunday et al., 2014). Throughout this article, we define *adaptation* as increasing fitness by evolving heritable genetic changes, whereas *acclimatization* and *acclimation* refer to changing phenotype in response to environmental drivers and experimental manipulations, respectively.

Similar to experimental results, the geological record of OA events that have occurred at various times during Earth's history (variously ascribed to a range of potential causes, including volcanism, destabilization of methane hydrates, oceanic anoxic events, and bolide impacts) suggests that many marine organisms and communities were negatively affected or may have even been driven to extinction by environmental changes associated with these perturbations (Hönisch et al., 2012). However, in many of these instances, it has not been possible to definitively attribute biological impacts to acidification alone, as pH shifts often occurred in concert with warming and anoxia. Furthermore, these events occurred over much longer time scales and at slower rates than anthropogenic OA (Zachos et al., 2005; Hönisch et al., 2012), which suggests that the current acidification event may have more severe outcomes than perturbations observed in the geological record (Hoegh-Guldberg et al., 2007; Pelejero et al., 2010).

Our theoretical understanding of nature is based on a body of observations, experiments, and models, some mathematical and some conceptual (Figure 1). Some aspects we understand well, while others we do not. Although we can accurately quantify what is observable (e.g., community composition for non-microbial organisms) and how this might change in response to certain environmental perturbations, in many cases we lack understanding of the underlying causal mechanisms responsible for the observed changes. In addition, we are often limited in terms of the spatio-temporal scales to which our results can be extrapolated. Even with advancements in imaging technologies and machine learning (Beijbom et al., 2012), the scales over which we can quantify community composition and structure remain somewhat limited. Building on the assumption that we have a relatively robust understanding of what the natural environment looks like, we still may not fully understand why it looks or functions the way it does.

The ultimate goal of contemporary OA research is to project how marine ecosystems will be affected by changes in seawater carbonate chemistry in combination with other perturbations, including warming, deoxygenation, eutrophication, and overfishing (Figure 1; Breitburg et al., 2015, in this issue). As new information is gained, hypothesis testing and validation refine our description of mechanistic pathways, bringing us closer to understanding nuances within the system. The projected ecosystem impacts and related socioeconomic consequences may motivate policymakers to (1) address the underlying problem (i.e., implement mitigation strategies such as reducing CO_2 emissions, pollution, overfishing, or eutrophication), (2) prepare for the associated changes (e.g., explore alternative resources and/or protect certain ecosystems), or (3) support research efforts to enhance both the understanding of current ecosystem status and function and the ability to predict how the ecosystem will respond to future changes so as to better inform policy decisions (Figure 1; Cooley et al., 2015, in this issue).

There is no doubt that ongoing anthropogenic OA will cause changes to many marine organisms and their communities. It also poses a challenge for scientists to make accurate and timely projections and recommendations for decision makers. To achieve these goals requires scientists to synthesize and integrate what we know from the geological record, laboratory and in situ manipulative experiments, studies in natural high CO_2 environments, and modeling studies, and to evaluate this information by considering the relevant rate of change and scale of the problem. To this end, we focus this article on the following questions:

1. What current OA research approaches are effective?
2. What are some of the major research challenges?
3. How can we improve our ability to make better projections of how marine ecosystems will change?

WHAT CURRENT OA RESEARCH APPROACHES ARE EFFECTIVE?

Ocean acidification was not fully recognized as a potential problem until about the year 2000, when a number of seminal papers highlighted the potential consequences associated with declining ocean pH (e.g., Kleypas et al., 1999; Caldeira and Wickett, 2003). Because of the initial oversight, OA has been referred to as the "other CO_2 problem," with the "first CO_2 problem" being that of global warming (Doney et al., 2009). The scientific community responded to the recognition of OA by convening a number of workshops, meetings, and conference sessions (e.g., High CO_2 World Meeting; Royal Society, 2005; Kleypas et al., 2006), organizing joint research efforts and consortia (e.g., European Project on OCean Acidification, EPOCA; Gattuso et al., 2009), publishing dedicated journal issues (e.g., *Marine Ecology Progress Series* vol. 373, 2008; *Oceanography* vol. 22(4), 2009, http://tos.org/oceanography/archive/22-4.html), and creating proposal opportunities by national funding agencies targeting OA. These early interdisciplinary efforts were critical to advancing our understanding of the impacts of OA and stimulating the increase in global research devoted to this problem. We now know much more than we did 10 years ago, but we still need to evaluate which research approaches are most effective and which should be changed in order to address the outstanding questions.

OA Research Approaches

Researchers have employed multiple approaches to study OA, including observations of natural environments experiencing different seawater CO_2 chemistry,

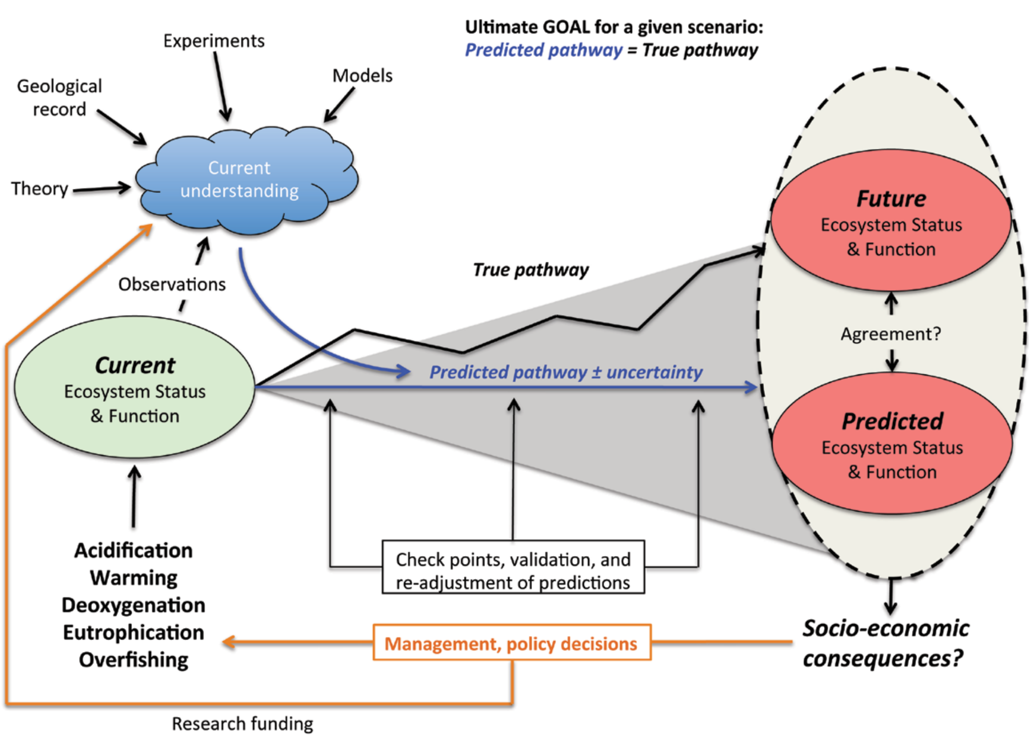


FIGURE 1. The current understanding (blue cloud) of ecosystem status and function is based on a range of research approaches, which form the foundation for predicting (blue lines) the effects of environmental perturbations such as acidification and warming on ecosystems. Ideally, the predicted pathway should equal the true pathway of how ecosystems will be affected by these perturbations, but in reality, the predictions are associated with an envelope of uncertainty (gray shaded area). Depending on the future predicted ecosystem status and function, socioeconomic consequences may warrant that policymakers address the underlying perturbations to reduce their impacts or alternatively allocate additional research funding to increase our understanding and improve future projections.

experimental manipulations in the laboratory and in the field, measurements from the geological record, and numerical model simulations (Table 1, Figure 2). Each of these approaches can be instructive in determining the potential consequences of OA, but each has limitations that must be recognized. Overall, this multifaceted approach to studying OA has enabled the research community to make great strides in a relatively short period of time. However, we believe that maintaining this progress will require increased interplay between approaches, with each being used to test hypotheses generated from the other approaches. The strengths and weaknesses of individual approaches are discussed below, along with how each approach has helped advance the field of OA research.

Observations from Natural Systems

To understand future effects of OA, it is necessary to understand current conditions, including natural controls and variability of seawater CO_2 chemistry, biogeochemical cycling, and environmental and ecological controls on organismal success. Establishing contemporary environmental conditions is necessary to evaluate future changes and impacts, and long-term time series are particularly useful in this regard. For example, time series stations (e.g., the Hawaii Ocean Time-series [HOT] and the Bermuda Atlantic Time-series Station [BATS]) and repeat basin-scale hydrographic research programs (e.g., the World Ocean Circulation Experiment [WOCE]) have been essential in detecting the ongoing decline in pH in the open ocean, but similar monitoring programs have until recently been largely missing from the coastal ocean. Understanding current conditions and their natural variability is critical in designing experimental manipulations that better reproduce the environmental ranges experienced by an organism (Table 1). Seawater carbonate chemistry (including pH) also vary naturally across temporal and spatial scales; these environments can be utilized to evaluate organismal and community functions across natural CO_2 gradients (e.g., Manzello et al., 2008; Hettinger et al., 2013). Some locations experience extreme CO_2 conditions that even exceed future levels expected from anthropogenic OA, as a result of volcanic CO_2 vents (e.g., Hall-Spencer et al., 2008; Fabricius et al., 2011), groundwater seeps (e.g., McGinnis et al., 2011; Crook et al., 2012), temporal isolation or stratification (e.g., Andersson et al., 2007, 2011), or upwelling events (e.g., Feely et al., 2008). Increasingly, these high CO_2 sites are being used for experimental studies to provide potential analogues to conditions in a future high CO_2 world.

The advantages of studies in natural systems are that they have the highest level of realism. Such approaches arguably are the best means for studying population and community effects, chronic effects, indirect effects, and ecological interactions.

TABLE 1. Relative strengths and limitations of different ocean acidification (OA) experimental approaches. Ratings are as follows:
1. – indicates the approach cannot be used for this purpose (as described in the Experimental Attributes column),
2. + indicates the approach can be used for this purpose and larger numbers of + signs indicate greater capacity to achieve the attribute, with ++++ being the best,
3. –/+ indicates that the approach is neutral, and
4. –/+++ or –/++++ indicates that the approach either cannot achieve the attribute or that it can depending on the experimental configuration.

	Experimental Attributes	Aquarium Studies	Mesocosms	In Situ Mesocosms	Benthic FOCE Type Studies	Vents & Seeps	Other Natural Gradients	Long-Term Sites
Experimental Design	Natural Realism	+	++	+++	+++	+++	+++	+++/?
	Replication	++++	++++	+++	+++	++	++	–
	Control Over Carbonate System Parameters	++++	++++	++++	++++	–	–	–
	Multiple Drivers	++++	++++	++	++	–/+	–/+	–/+
	Cost	+++	+++	+	+	++/+++	++/+++	++
Types of Studies	Effects on Individuals	++++	+++	+++	+++	++	++	+++
	Population and Community Effects	–	+/++	+++	+++	++++	++++	++++
	Acute Effects	++++	++++	+++	+++	+++	+++	–
	Chronic Effects	++++	+++	+++	+++	++++	++++	++++
	Direct Effects	++++	+++	+++	+++	+++	+++	+/–
	Indirect Effects	–	+++	+++	+++	++++	++++	++++
Evolution	Adaptation	++++	–/+++	–/+++	–/+++	–/++++	–/++++	–/++++
	Acclimation	++++	++++	++++	++++	++	++	–
	Acclimatization	+	+	++	++	++++	++++	++++

Moreover, they can be good for studying acclimatization and adaptation of sessile organisms (Table 1). For both mobile and sessile organisms with planktonic larvae, it is more challenging to study adaptation, as migration and immigration make it difficult to determine exposure histories and the conditions under which organisms evolved. The major disadvantages of natural studies are limited replication, lack of true controls, inability to manipulate carbonate system parameters and to distinguish between multiple drivers, and the potential for seawater chemistry that is not representative of other oceanic environments.

Experiments and Manipulations

Manipulating seawater CO_2 under controlled conditions in the laboratory or in the field is the only way to create and evaluate the responses of organisms or communities to specific conditions anticipated for the future. It is also probably the most viable approach to establishing functional relationships (response curves) for different organismal traits and seawater CO_2 chemistry, which are essential for parameterizing numerical models. A number of approaches have been used to manipulate seawater carbonate chemistry, ranging from bubbling with CO_2 gas to adding acid or bases to experimental setups (Gattuso and Lavigne, 2009). Most experimental manipulations have been conducted at relatively small scales with individual species or micro communities, while a smaller number of experiments have been conducted in mesocosms with larger representation of natural communities (Jokiel et al., 2008, Riebesell et al., 2008, 2013; Dove et al., 2013; Tatters et al., 2013; Comeau et al., 2014). Some of these mesocosms have been designed and developed for deployment in the natural environment (Yates and Halley, 2006; Riebesell et al., 2008). Recently, a number of groups have developed benthic Free Ocean Carbon Enrichment

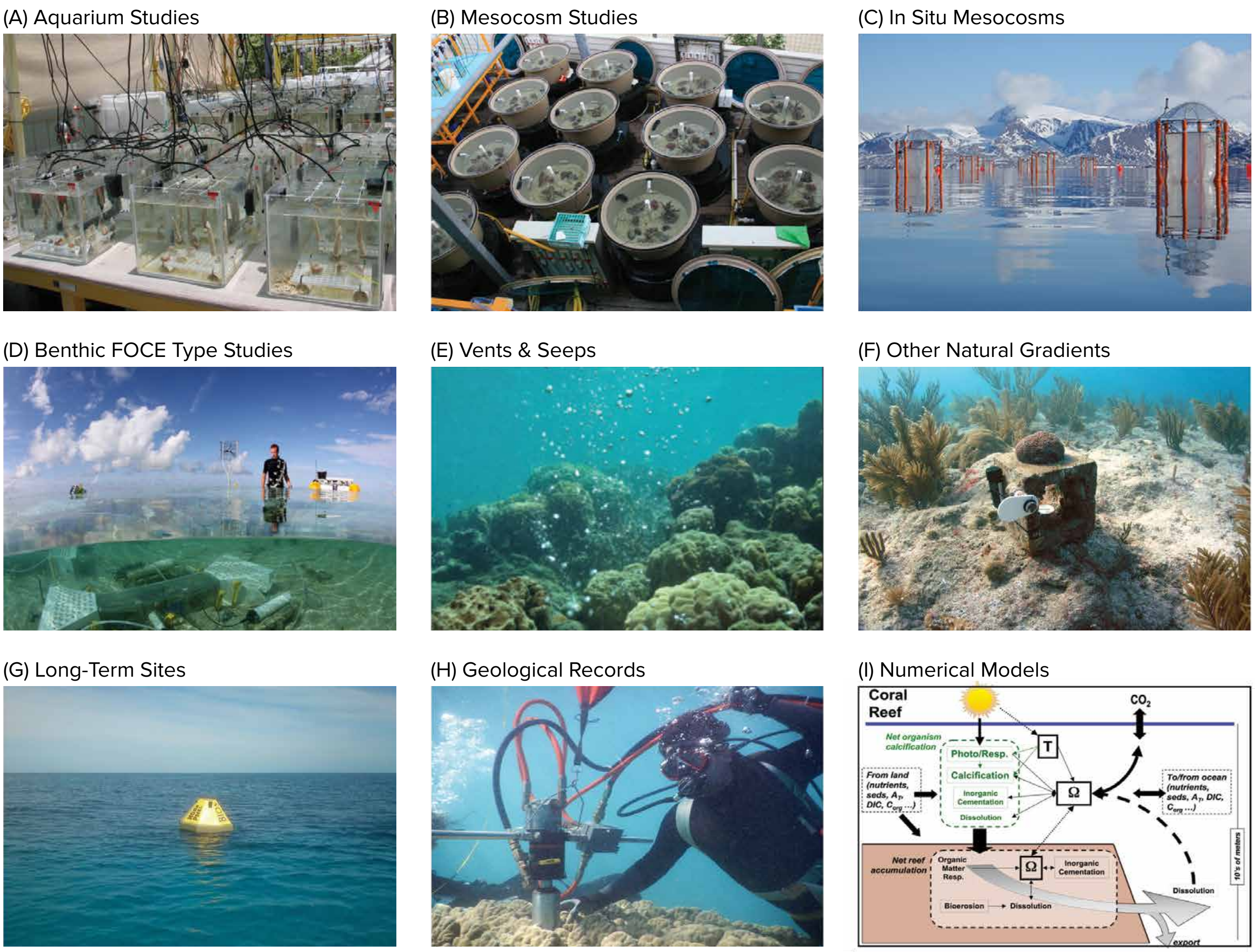


FIGURE 2. Summary of experimental approaches used in ocean acidification research. Each experimental approach has strengths and limitations (Table 1), and a combination of approaches at different spatial and temporal scales is needed to advance our understanding of molecular- to ecosystem-level impacts. The image in (C) is courtesy of Signe Klavsen, GEOMAR, (E) from Fabricius et al. (2011) with permission from *Nature Climate Change*, (H) courtesy of Curt Storlazzi, US Geological Survey, and (I) from Kleypas et al. (2006), courtesy of Joanie Kleypas, NCAR. All other images are originals taken by one of the authors.

(FOCE) systems to evaluate the effects of OA in situ while maintaining tight control over carbonate chemistry conditions (Kline et al., 2012; Barry et al., 2014; Gattuso et al., 2014).

Each of the experimental approaches has advantages and limitations. Small-scale aquarium studies are effective in allowing for high levels of replication and control over carbonate system parameters (Table 1). They are ideal for multiple-driver studies and are relatively cost effective. They are excellent for studying acute, chronic, or direct effects of OA on individual species or mixed microbial populations, and they are used for adaptation and acclimation studies of organisms with short generation times. The major limitation of small-scale studies are that they have reduced levels of natural realism, as the organisms are removed from the environment and placed in a container filled with varying volumes of seawater. Such approaches are less useful for studying populations and communities (depending on the sizes of the organisms) or indirect effects. Mesocosm studies have many of the same strengths and weaknesses of small-scale aquarium studies, but they have the added advantage that communities at the macro scale can be constructed within them to enable studies of population/community impacts. In situ mesocosms such as the floating structures developed by Riebesell et al. (2012) offer increased realism that improves researchers' ability to study population/community impacts as well as aspects of biogeochemistry, like carbon flux. However, compared to small-scale aquarium studies, these experiments are more challenging and more costly, and constitute a more difficult approach for achieving sufficient statistical replication and for studying multiple driver impacts. Benthic FOCE-style studies similarly increase natural realism, can be used to study population and community effects under controlled carbonate chemistry conditions, and allow assessment of both direct and indirect effects. However, like use of in situ mesocosms, this experimental approach is elaborate and relatively costly and has so far required high levels of funding and collaboration for success.

Geological Record

The geological record may hold many clues to the potential impacts of current and future OA, as there have been several CO_2 perturbation events throughout Earth's history. Data about past conditions are obtained by recovering sediment and ice cores through drilling. Sediment samples that include the skeletons of microscopic animals are analyzed for species assemblages and elemental isotopes. These data, as well as many other proxies, provide information about the environmental conditions at the time the biota were deposited. However, a suitable analogue to the current human-driven decline in oceanic pH and carbonate saturation state from the geological record needs to be found. Unfortunately, the geological record provides no evidence of an event with a comparable rate of change as is presently occurring, and high-resolution (annual to decadal) records for much of the geological record are not attainable. The Paleocene Eocene Thermal Maximum (PETM) provides perhaps the best analogue to current OA. Occurring 55 million years ago, the PETM involved the release of a quantity of CO_2 comparable to that expected from anthropogenic sources since the Industrial Revolution and in the next centuries. Analysis of sediment cores reveal that the PETM was associated with the extinction of many species of deep-sea foraminifera and shoaling of the maximum depth where $CaCO_3$ accumulated in the sediments (Kump et al., 2009), features that are consistent with a decrease in the carbonate saturation state of the ocean at that time. However, the PETM CO_2 event occurred over a few thousand years, compared to a few hundred years expected for the current case (Zachos et al., 2005; Kump et al., 2009), which limits its analogy to the OA event happening today.

While still in its infancy, the use of proxy records for reconstructing paleo-pH and other carbonate parameters (and corresponding response variables) from the geological record is another approach to understanding OA impacts (e.g., Dissard et al., 2012; Liu et al., 2014). As with the natural-experimental approaches, it is challenging to disentangle the effects of multiple environmental variables that are correlated, but a multi-proxy approach could help in this regard (Levin et al., 2015, in this issue).

Numerical Model Simulations

Numerical modeling is vital for integrating and conceptualizing our current understanding of OA in order to generate predictions about future effects on marine ecosystems. It is also important for testing hypotheses, evaluating the sensitivity of different parameters, identifying knowledge gaps, and guiding observational and experimental studies. However, the accuracy of any model prediction is dependent on the accuracy of the input data and the representative equations used to simulate processes. Hence, modeling efforts are dependent upon, and limited by, the quantity and quality of data generated from experimental and natural studies. Moreover, while validation of model predictions against independent observations is necessary to evaluate model performance, it is not always possible. Some examples of numerical modeling efforts to date include predicting open ocean pH and the depths of aragonite saturation horizons under different CO_2 emission scenarios (Joos et al., 2011; Hauri et al., 2013), hindcasting historical seawater chemistry (Ridgwell and Zeebe, 2005), evaluating future coral reef calcification and accretion (Silverman et al., 2009), examining acidification-mediated climate feedback through changes in trace gas emissions (Six et al., 2013), and assessing the feasibility of ocean alkalinization as a potential mitigation strategy (Ilyina et al., 2013).

RESEARCH CHALLENGES AND THE WAY FORWARD

In spite of substantial efforts using a wide range of research approaches, there are still many outstanding knowledge gaps and challenges that need to be overcome to improve our projections of how ecosystems will change in response to OA. Some of these challenges involve evaluating the effect of OA in the context of large natural variability in carbonate system parameters and other interactive variables (Breitburg et al., 2015, in this issue), integrating results from different research approaches, and scaling results across different temporal and spatial scales.

Regional Changes and Natural Variability

The effects of OA on marine communities and ecosystems vary among geographic regions owing to local climate, hydrography, seawater chemistry, nutritional status, proximity to land and human influences, biodiversity, and the resistance and resilience of ecosystems. So far, most research has focused on the responses of organisms to near constant pCO_2, guided by IPCC emission scenarios and pCO_2 values predicted for open-ocean surface water over the next few centuries. Nearshore environments, however, are different from open-ocean conditions, with large changes in seawater chemistry on both diel and seasonal time scales with extreme pCO_2 values often exceeding those predicted for the open ocean by the end of the current century (Hofmann et al., 2011; Andersson and Mackenzie, 2012; Duarte et al., 2013; Kline et al., in press). Emerging evidence from a small number of experimental studies suggests that diel and seasonal variability can dramatically affect organismal responses to OA (e.g., Dufault et al., 2012; Johnson et al., 2014). For example, Johnson et al. (2014) exposed coralline algae to oscillating and elevated pCO_2 treatments and showed that individuals collected from a site with naturally high variability maintained higher rates of calcification compared to individuals collected from a site of low variability. They proposed that individuals from the high variability environment might already be acclimatized to OA within the range of the natural variability they experience. Thus, the fact that many organisms experience large diel and seasonal variability in carbonate chemistry raises several critical questions including:

- How do organisms and communities respond to both large fluctuations and episodic exposure to high pCO_2 and low pH values?
- Are organisms from variable environments better adapted to respond to OA compared to organisms living under more stable conditions?
- Are there physiological and ecological thresholds beyond which organismal and ecosystem susceptibility to further OA is acute? If so, are the magnitude and duration of these conditions more important than their mean in determining organismal responses to OA? How can these thresholds be identified?
- What is the potential for acclimatization and adaptation to OA over the next few centuries? Will current physiological thresholds for organisms change, if so, how fast, and to what extent could these changes occur?

The large temporal and spatial variability in OA conditions observed in nearshore environments occurs as a result of biological processes, including photosynthesis, respiration, calcification, and calcium carbonate dissolution, as well as inputs of carbon and other nutrients from upwelling, terrestrial runoff, groundwater, and rivers. To accurately predict future changes in the coastal ocean as a result of OA, we need to better understand the range and variability of seawater carbonate chemistry, the factors controlling this variability, the extent to which it can be attributed to natural versus anthropogenic drivers, and co-variation with other environmental variables (Duarte et al., 2013; Reum et al., 2015). Importantly, we have not unequivocally observed an anthropogenic OA trend over time in coastal environments. This is partly due to the large natural variability in these environments and the lack of suitable instrumentation to fully constrain seawater carbonate chemistry. In addition, there have been limited time-series observations of sufficiently long duration to detect a coastal OA trend as a result of rising atmospheric CO_2. Research and management of coastal ecosystems will require the incorporation of new monitoring technologies for regional and local efforts (Martz et al., 2015, in this issue) because ecosystem metabolism and watershed processes exert strong effects on coastal seawater chemistry (Duarte et al., 2013).

OA will alter the mean carbonate chemistry conditions in most marine environments, but the observed natural variability of seawater pCO_2 and pH will increase due to reduced buffering capacity of the seawater carbonate system under elevated pCO_2 conditions (assuming total alkalinity remains constant; Shaw et al., 2013). Due to the large variability in many natural systems, there is a strong need for physiologists to ground their experimental analyses in ecologically relevant conditions defined by the natural range of pCO_2 and pH values, as well as the temporal scale of natural variation (Figure 3). More experiments should use controls that mimic natural conditions and variability with treatments established as offsets from these conditions (e.g., Jokiel et al., 2008; Kline et al., 2012; Dove et al., 2013). For some environments (e.g., upwelling regions), it is also important to consider co-variation with other variables such as temperature and oxygen (Reum et al., 2015).

Integration of Results

Comparison and integration of results are important because consistent agreement between different or replicated approaches improves our understanding and confidence in the effects of OA on marine ecosystems (assuming that the various approaches are sufficiently diverse that they do not contain a systematic bias). Diverse experimental approaches contribute different aspects of understanding and can provide additional guidance for improving the design of other approaches (Figure 1). For example, small-scale experimental studies provide information on organisms' physiological responses to different pH conditions that can be incorporated as functional relationships in models. Observational field studies document the natural variability in carbonate chemistry conditions that organisms currently experience, which is essential for developing ecologically relevant experimental treatments. Mesocosm and FOCE studies bridge the gap between small-scale lab experiments and field observations where interpretations are complicated by confounding factors. Geological observations provide information about past OA events and their consequences, which can improve our understanding of experimental and modeling predictions. Finally, numerical models play an important role, as they provide a means to integrate functional relationships with both current and future conditions to generate predicted outcomes that can be used for the testing of hypotheses and identification of knowledge gaps. If we want to scale up to ecosystems, we need to involve modelers early on and in close collaboration with experimental and observational efforts. It is also important that the strengths and limitations of each experimental approach be considered when integrating results across studies (Table 1). The limitations of each approach should be critically evaluated so that interpretation of data does not overreach, and so that results can be reasonably scaled and extrapolated.

In cases of contradicting or radically different outcomes between studies, significant effort should be devoted to identifying the underlying reasons for these discrepancies and whether they represent true functional differences or experimental artifacts. Best practices in terms of the characterization of the dominant physical, environmental, and chemical parameters and their variability are important to avoid discrepancies and confusion arising from incompletely characterized systems (Figure 3). The same is true for characterizing the response variables in organisms and ecosystems (Riebesell et al., 2010). Response variables should be expressed as "common currency" units so that results can be compared across studies. For example, expressing calcification rates on a planar surface-area basis could provide cross validation among functional response experiments, whole-reef metabolic measurements, and numerical modeling studies.

Proper data characterization and reporting also facilitate meta-analysis, which aims to evaluate the results from multiple studies based on statistical methods. Several meta-analyses have been conducted in the context of OA (Hendriks et al., 2010; Kroeker et al., 2010; Liu et al., 2010; Chan and Connolly, 2013; Kroeker et al., 2013). By combining the results of multiple studies, meta-analyses increase the sample size and therefore the statistical power with which to test a particular effect. However, they are limited by the selection of studies used and the inherent biases in this selection. The major sources of bias include publication bias, or the tendency to publish papers showing conclusive results so that inconclusive results rarely get published; search bias, or the possibility that relevant studies are excluded because they were overlooked or reported data insufficiently; and selection bias, which can occur if the criteria for including and excluding studies are not well defined (Walker et al., 2008; Gattuso et al., 2011).

Scalability of Results

One critical need of OA research is the ability to apply experimental results to natural systems and to link results and processes operating at different temporal and spatial scales. Many experiments are limited in space and time, and generally do not capture natural ecological interactions (e.g., competition, trophic feedback, synergistic and antagonistic effects). How can we account for these ecological interactions and integrate results from organizational scales that range from cellular/molecular to species/cultures to populations to ecosystems and to global elemental cycles (Figure 4)? How can results from these seemingly disparate approaches be used to conclude something about the effects of OA on ecosystems and global elemental cycles? A combination of research approaches can provide mechanistic understanding at a range of scales. Care must be taken when scaling results from small to larger experiments, and the

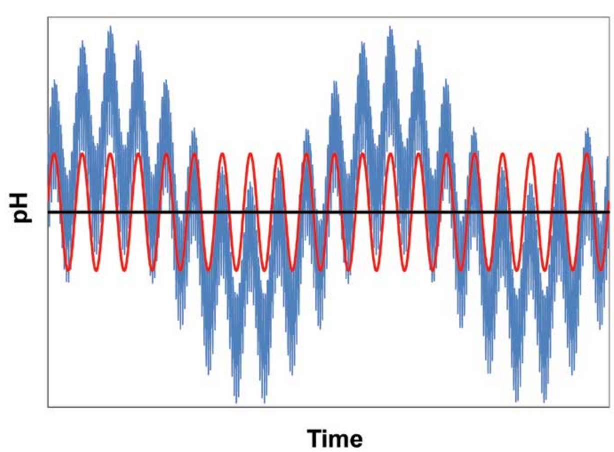
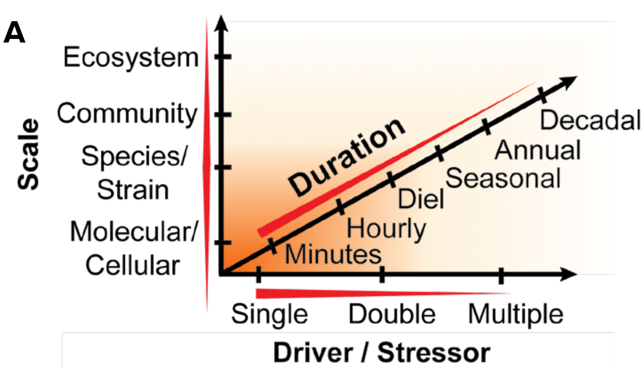


FIGURE 3. Three examples of pH variation through time (but it could be any environmental or chemical parameter). Black line indicates a constant pH, with no measurable variation through time. Red line indicates a periodic signal of constant frequency and amplitude driven by a single oscillator (e.g., photoperiod) with the same mean as the black line. Blue line indicates the combined effects of multiple oscillators (e.g., photoperiod, tide) producing a complex temporal pattern with the same mean as the black line. It is critical that experimental and observational studies consider the natural variability, as it will influence physiological and ecological responses, as well as being critical for determining the proper carbonate chemistry sampling regime.

caveats should be rigorously considered and reported. Especially in the early days of OA research, results obtained from small-scale aquaria were commonly used to infer what might happen at the global scale. For example, observed decreases in calcification rates of corals, mussels, and other calcifiers were extrapolated to the global scale under projected pH conditions (Andersson et al., 2005; Cooley and Doney, 2009). However, the sum of the parts is not necessarily equal to the whole; for example, a 10% decrease in the calcification of an adult coral colony owing to a 0.1 unit decrease in pH does not necessarily translate to a 10% reduction in coral community growth. Direct extrapolation is often a first approach to evaluating the global impact of a newly discovered problem. While this can be an effective start, it is most certainly not an effective end, as it is unlikely that the responses of organisms ex situ or the responses of a few isolated species will accurately reflect ecosystem responses on a global scale (Figure 4).

Instead of a simplistic extrapolation, more refined and integrative approaches will be necessary. They involve the development of a fundamental understanding of how results at different scales are linked and can be scaled to one another, both from small to larger scales, and large to smaller scales. These are not trivial tasks, but several approaches are already available for establishing rigorous links between different scales of investigations. In general, striving for a mechanistic understanding and addressing the question of "why" a certain response was observed at any given level is likely to facilitate accurately scaled predictions. For example, addressing why some corals calcify more slowly than others at lower seawater pH may be illuminated by considering molecular, cellular, and physiological responses along with local environmental and carbonate chemistry conditions where the particular corals live. Similarly, an observed decrease in net community calcification in response to lower pH may be due to decreased calcification, increased $CaCO_3$ dissolution, or a combination of both. In most cases, striving for mechanistic understanding requires elegant experimental designs within hypothesis-driven frameworks that facilitate analyses of multiple properties and organisms at various scales.

To scale up results to the level of ecosystems, it is helpful to have access to physiological, ecological, and biogeochemical time series observations. The data essential for establishing some of these time series are being collected by HOT and BATS, Long Term Ecological Research networks (LTERs), the National Estuarine Research Reserve System (NERRS), and other time-series monitoring programs, and they may also be retrieved from historical records. Although it may take decades for important trends to become apparent from such data sets, they are absolutely critical to advancing our knowledge in the long run. In this context, it is particularly relevant to acknowledge the lessons learned by Charles David Keeling's persistence in maintaining long-term, high frequency observations of atmospheric CO_2 (http://scrippsco2.ucsd.edu/program_history/keeling_curve_lessons.html). Furthermore, to facilitate scaling to ecosystems, we argue that using a collaborative laboratory-field-modeling team approach has great potential for success. This approach facilitates focused and complementary research results that are likely to advance the field. It will force researchers to focus on key limitations, including critical species and ecological interactions, and to attempt to fill those gaps.



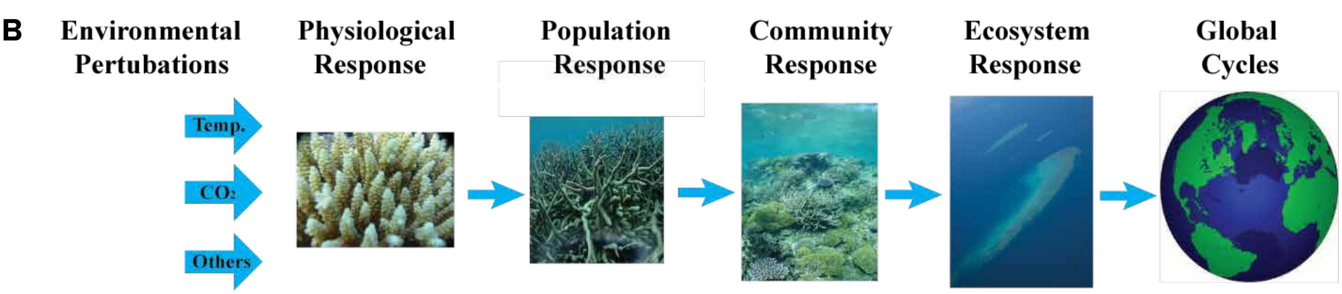


FIGURE 4. (A) Representation of how multiple drivers, spatial scales, and duration of exposure to stressors combine to determine the impacts of OA. The width of the red arrows indicate the amount of current knowledge about OA impacts and emphasize that we currently know the most about single species/strains affected by one driver for an acute duration. To better understand OA impacts, we need to move toward studying multiple drivers at a range of scales and a range of durations. Clearly, much future work will be needed to integrate results that properly consider multiple drivers at various spatial and temporal scales in order to better understand mechanisms and ecosystem level impacts. (B) The challenge of scale. These figures highlight the range of scales that must be considered to study the impacts of ocean acidification on molecular to global scales.

This will be spurred by dedicated opportunities that foster interdisciplinary and integrative research efforts. To truly advance the field, we need to develop paradigms to link and integrate multiscale and multi-approach data, which is critical for gaining synthetic capacity. Otherwise, there is a danger of progressing further down a phenomenological road and accumulating facts that cannot be assembled into a coherent story. Theory is a critical piece of this research puzzle, and its application will be essential to developing hypothesis-driven approaches that will be of use in the next phase of OA research.

Building on Previous Knowledge

To ensure advancement in our understanding of the impacts of OA, we need to avoid undue emphasis on reinventing the wheel in terms of definitions, concepts, and approaches. A lot of important information and knowledge is available to assist in addressing stress responses of organisms to a variety of factors, including information regarding ecotoxicology issues from the 1980s that seem very relevant to addressing OA effects (Levin et al., 1989).

As an example, many core questions relevant to understanding the effects of OA on coral reefs (and other marine ecosystems) fall in the domains of physiology, molecular biology, community metabolism, and oceanography. A deeper understanding of the effects of OA on calcification of reef corals requires knowledge of cellular and subcellular processes (i.e., physiological events) that mediate the union of Ca^{2+} and CO_3^{2-} to support the deposition of aragonite skeletons ($CaCO_3$). At the most fundamental level, these events are ultimately under genetic control and their effects cascade across functional levels to mediate the gross calcification of the reef (i.e., community metabolism) through physical and chemical interactions with the surrounding seawater (i.e., oceanographic processes). Scientists with classic training in these domains have the potential to make rapid progress in answering fundamental questions of scientific and societal importance, and the same is true for other important marine ecosystems.

Evaluating the structures and functions of marine ecosystems in a warmer and more acidic ocean requires forging conceptual bridges to couple the information from multiple research domains. Identifying, codifying, and quantifying these bridges is one of the most important challenges facing the community of scientists engaged in OA research. It is important that these efforts do not neglect progress with similar objectives in other areas of biological research. There is, for instance, a very rich history of studying scale dependency in physiological and ecological processes (Levin, 1992), the causes and implications of community resilience and stability (Gunderson, 2000; Petraitis, 2013), and the role of density feedback mechanisms in mediating ecological processes (Sale and Tolimieri, 2000).

Future OA research will require the broad participation of scientists with complementary skills to address emerging questions focusing on the profound ways in which humans are perturbing the natural environment (Yates et al., 2015, in this issue). The research community is learning a lot, but we are currently limited in our ability to assess emergent properties, to leverage important breakthroughs, and to promote insightful and effective resource management. These potential objectives are not mutually exclusive, and it is safe to conclude that most people do not want to oversee the widespread demise of marine ecosystems. Thus, it is important to explore potential solutions to OA as we seek to better understand the problem.

CONCLUSIONS

- The effects of OA, in combination with other environmental perturbations (e.g., warming, eutrophication, deoxygenation), on marine ecosystems and elemental cycles are specific to geographical regions, species, and ecosystems. Future experiments need to incorporate observed natural environmental variability into experimental treatments to enhance the generality of the results.
- No one research approach to addressing the effects of OA on marine ecosystems is superior to others. Instead, a diverse combination of approaches is essential to address this problem, as long as the limitations of each approach are recognized and considered.
- Experiments need to be performed at a range of spatial scales, from molecular to ecosystem, and at a range of temporal scales, from minutes to decades. The scalability of results is critical to improving understanding of OA impacts across larger temporal and spatial scales (e.g., years to decades to centuries, and community to ecosystem to global scales).
- We should aim to integrate results and bridge between different scales in order to build a stronger conceptual understanding of ocean acidification. This involves collaborating across different disciplines and striving to develop mechanistic understanding of the underlying processes.

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