Food for Thought

The challenges of detecting and attributing ocean acidification impacts on marine ecosystems

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A substantial body of research now exists demonstrating sensitivities of marine organisms to ocean acidification (OA) in laboratory settings. However, corresponding in situ observations of marine species or ecosystem changes that can be unequivocally attributed to anthropogenic OA are limited. Challenges remain in detecting and attributing OA effects in nature, in part because multiple environmental changes are co-occurring with OA, all of which have the potential to influence marine ecosystem responses. Furthermore, the change in ocean pH since the industrial revolution is small relative to the natural variability within many systems, making it difficult to detect, and in some cases, has yet to cross physiological thresholds. The small number of studies that clearly document OA impacts in nature cannot be interpreted as a lack of...
larger-scale attributable impacts at the present time or in the future but highlights the need for innovative research approaches and analyses. We summarize the general findings in four relatively well-studied marine groups (seagrasses, pteropods, oysters, and coral reefs) and integrate overarching themes to highlight the challenges involved in detecting and attributing the effects of OA in natural environments. We then discuss four potential strategies to better evaluate and attribute OA impacts on species and ecosystems. First, we highlight the need for work quantifying the anthropogenic input of CO₂ in coastal and open-ocean waters to understand how this increase in CO₂ interacts with other physical and chemical factors to drive organismal conditions. Second, understanding OA-induced changes in population-level demography, potentially increased sensitivities in certain life stages, and how these effects scale to ecosystem-level processes (e.g. community metabolism) will improve our ability to attribute impacts to OA among co-varying parameters. Third, there is a great need to understand the potential modulation of OA impacts through the interplay of ecology and evolution (eco–evo dynamics). Lastly, further research efforts designed to detect, quantify, and project the effects of OA on marine organisms and ecosystems utilizing a comparative approach with long-term data sets will also provide critical information for informing the management of marine ecosystems.

**Keywords:** anthropogenic CO₂ contribution, coral reefs, ecological-evolutionary dynamics, ecosystem trajectory, oysters, pteropods, seagrass

**Introduction**

A third of the anthropogenic CO₂ released to the atmosphere has been absorbed by the oceans, causing declines in ocean pH and calcium carbonate saturation state (Bindoff et al., 2019; Gruber et al., 2019). These changes are referred to as ocean acidification (OA) (Caldeira and Wickett, 2003; Doney et al., 2009; Le Quéré et al., 2018). Information from the geological record (Hönisch et al., 2012), laboratory experiments (Kroeker et al., 2013), field observations (Keller et al., 2014; Sutton et al., 2016, 2017; Henson et al., 2017; Turk et al., 2019), and numerical modelling (Marshall et al., 2017) strongly suggests that OA has the potential to alter the function of ocean ecosystems, impacting marine biota and ecosystem services (Andersson et al., 2015). However, characterizing current and future effects of OA on marine systems is challenging. While there is a general consensus that OA elicits largely negative effects on calcifying organisms and positive effects on primary producers (Kroeker et al., 2010; Busch and McElhany, 2016; Mostofa et al., 2016), these conclusions are primarily drawn from laboratory experiments in which species sensitivity is evaluated using short-term incubations under elevated CO₂ conditions. Controlled experiments have found relationships between organism responses and CO₂ conditions (Waldbusser et al., 2014) and have considered how physiological sensitivities scale to predictions of evolutionary responses (Munday et al., 2013). These types of studies offer important insight into mechanistic responses of marine organismal physiology to OA but may provide a limited assessment of population-level impacts due to the complexity of how OA impacts may cascade through ecosystems (e.g. variation in the sensitivity of individuals within a community and subsequent impacts on population dynamics; Busch et al., 2013; Busch and McElhany, 2016). In addition to characterizing existing organismal sensitivities to OA, we must document how ecologically complex in situ conditions (e.g. simulating natural variability of carbonate chemistry, food availability) vary from those observed in the laboratory to understand OA impacts and interpret ecosystem-level responses (Andersson and Mackenzie, 2012). OA sensitivities are also expected to vary widely in natural systems, for example an average 0.1 decline in pH due to OA could be enough to push some species or ecosystems over critical thresholds, or might be unimportant in systems that have natural variability ranging from 0.5 to 1 pH units within a day (Hofmann et al., 2011).

Challenges of both spatial and temporal scaling of laboratory results to in situ responses are compounded by the need to understand how OA interacts with other physical, chemical, and biological forcings (Breitburg et al., 2015; Kroeker et al., 2017). While researchers generally agree that a multifaceted approach is necessary, evaluating the benefits and drawbacks of different approaches requires careful consideration (see Andersson et al., 2015; Boyd et al., 2018). For example, free ocean carbon enrichment-type experiments constrain natural variation between specific locations within an ecosystem while only manipulating CO₂ (Barry et al., 2014;Gattuso et al., 2014; Doo et al., 2019) but are difficult to scale to ecosystem-level projections of OA impacts. Furthermore, in situ large-scale pelagic mesocosms studies have been performed to document changes in plankton communities, although the community composition and trajectory (e.g. potential phytoplankton blooms in select mesocosms) are difficult to constrain (Bach et al., 2016; Algueró-Muniz et al., 2017; Riebesell et al., 2017, 2018). Field-based observations are largely gleaned from natural CO₂ gradients (from vents/seeps and spatial pH gradients) across ecosystem scales (e.g. Hall-Spencer et al., 2008; Fabricius et al., 2011; Silbiger et al., 2014; Barkley et al., 2015; Mollica et al., 2018). However, these effects are often interwoven with other physical and chemical parameters that are difficult to disentangle (Silbiger et al., 2017). Other methods, including statistical techniques (e.g. Silbiger et al., 2014) and proxies (e.g. Mollica et al., 2018), have been used to gain insight into how ecosystems may respond to OA. Scaling between sensitivity information from laboratory settings to multi-generational and ecosystem-level responses in nature has largely been done using conceptual models (Busch et al., 2015; Edmunds et al., 2016). These models are complemented by laboratory studies that assess potential transgenerational adaptation effects, highlighting the possibility for organisms to rapidly adapt to changing CO₂ conditions (Parker et al., 2015; Putnam and Gates, 2015; Wong et al., 2018). Although both natural and laboratory experiments strongly suggest negative biological consequences in response to OA, long-term (multi-decadal) biological and ecological measurements that are unequivocally linked to anthropogenic CO₂ accumulation in situ are limited to a handful of studies, mostly on planktonic foraminifera (de Moel et al., 2009; Moy et al., 2009; Fox et al., 2020; Osborne et al., 2020).

Disentangling effects of OA on marine species from natural environmental variability and other climate change drivers has been a cornerstone of OA research over the past decade (Breitburg et al., 2015). The quality and abundance of ocean carbonate chemistry measurements have advanced, making progress in attributing ocean chemistry changes to anthropogenic CO₂ (Weisberg et al., 2016). Although OA has been unequivocally
observed in the open ocean (Bates et al., 2014), this trend is only beginning to be documented in near-shore environments due to high natural variability and limited duration of observations (Duarte et al., 2013; Andersen et al., 2015; Reimer et al., 2017; Sutton et al., 2019). Time of emergence refers to the point at which an anthropogenic signal is detectable outside the bounds of natural variability; it has been applied with success to marine carbonate chemistry and other oceanographic measurements of CO₂ increase (Keller et al., 2014; Sutton et al., 2016, 2017; Henson et al., 2017; Turk et al., 2019), but has not been observed in some ocean environments, especially those lacking historical measurements, including many coastal regions (Sutton et al., 2019). With many marine ecosystems lacking time-series measurements of carbonate chemistry and biological indices that are longer than the time of emergence, the extent to which biological responses are attributable to OA in nature remains an open question.

The topic of scaling from laboratory-based, single-species studies to understanding OA impacts in situ has been discussed in previous perspectives and syntheses (Hennige et al., 2014; Riebesell and Gattuso, 2015; Hurd et al., 2018). Our aim here is to review our ability to detect and attribute OA impacts for four well-studied groups and to stimulate further discussion and consideration of how to improve detection and attribution as the OA research field continues moving forward. Here, we refer to OA sensitivity as any biological response (physiological change) of an organism to increasing CO₂. An impact of OA is defined as a change in an in situ biological measurement that is attributed to in situ changes in seawater chemistry resulting from increasing anthropogenic CO₂. We focus on four groups (seagrasses, pteropods, oysters, and coral reefs), selected for their sensitivity to OA and their ecological and/or economic importance. The authors also have expertise in each of these groups. For each, we summarize the results of laboratory and field-based studies on CO₂ sensitivity and the current ability to detect and attribute change in the system to OA. The complications discussed here are not meant to criticize existing studies but to highlight the need for a greater understanding of the impacts of OA in natural ecosystems and for an improved ability to attribute and quantify these impacts.

Seagrasses

Seagrasses are commonly considered potential beneficiaries of OA; they are carbon-limited under current CO₂ conditions and increase photosynthesis under higher CO₂ concentrations (Koch et al., 2013). This is in contrast to most marine autotrophs, which have developed efficient strategies for utilizing bicarbonate (HCO₃⁻), and is due to the relatively recent evolution of marine seagrasses under comparatively higher CO₂ concentrations (Beer and Koch, 1996; Zimmerman et al., 1997). Results from mesocosm and in situ manipulations of CO₂ indicate increased seagrass productivity, shoot density, and biomass under elevated CO₂ conditions (Beer and Koch, 1996; Zimmerman et al., 1997; Hall-Spencer et al., 2008; Fabricius et al., 2011; Campbell and Fourqurean, 2014). However, divergent results have been found in volcanic CO₂ seep sites. Seagrasses in the Mediterranean show decreases in density and biomass (Apostolaki et al., 2014) and in Papua New Guinea have up to a fivefold biomass increase (Takahashi et al., 2016) with increasing CO₂. In addition, seagrass species live in a complex environment; thus, seagrass response to OA will likely be modulated by interactions with other species. For example, a decrease in calcareous epiphytes on seagrasses at CO₂ seeps has been shown (Martin et al., 2008), while the potential for an increase in fleshy epiphytes has also been documented (Campbell and Fourqurean, 2014). Globally, seagrass abundance has declined by ~30%, which has been attributed to coastal urbanization, rising sea surface temperatures, and water quality degradation (Waycott et al., 2009).

To our knowledge, no in situ study has attributed positive effects of anthropogenic OA on seagrass growth, while decreases in species density and range have been observed in response to other anthropogenic stress (e.g. pollution, warming; Koch et al., 2013). Furthermore, theoretical OA refugia created by seagrasses have not yet been observed consistently in situ and are likely dependent on site-specific factors (e.g. residence times, autotroph location relative to water advection, community composition) making successful in situ attribution of benefits to adjacent calcifiers difficult (Anthony et al., 2011, 2013; Unsworth et al., 2012; Mongin et al., 2016). In addition, although photosynthesis by seagrasses decreases CO₂ during the day, potentially equal or greater night-time respiration may counteract daytime effects by increasing CO₂, resulting in a near-zero daily balance that produces negligible effects on the progression of OA (Koweek et al., 2018; Pacella et al., 2018; Kapsenberg and Cyronak, 2019). While the theoretical benefits of OA on seagrass growth have been well documented in the laboratory, it appears that substantial negative impacts from other anthropogenic stressors may counteract any positive effects of increased CO₂ and have likely prevented the isolation and attribution of the potential beneficial responses of OA (Koch et al., 2013).

Pteropods

Pteropods were one of the first taxonomic groups identified as vulnerable to OA (Orr et al., 2005). Numerous laboratory experiments have documented negative effects of exposure to elevated CO₂, including shell dissolution, reduced (or absent) calcification, altered respiration rates, decreased sinking rates, differential gene expression, delayed egg development, and increased mortality (Comeau et al., 2009, 2010a, b; Lischka and Riebesell, 2012, 2017; Manno et al., 2012, 2016; Seibel et al., 2012; Busch et al., 2014; Koh et al., 2015; Maas et al., 2015; Thabet et al., 2015; Moya et al., 2016; Johnson and Hofmann, 2017). However, the response of pteropods to high CO₂ is not uniformly negative (Maas et al., 2016), and the outer organic layer of the pteropod shell offers some protection from undersaturated waters (Peck et al., 2016, 2018).

OA-related pteropod field observations have focused on a variety of time scales and response metrics. Analysis of pteropod shell collections from the past 100 years in the Mediterranean show declines in shell thickness and density for two different species (Howes et al., 2017). Sediment core studies indicate some evidence for a correlation between fossil pteropod shell dissolution during life and atmospheric CO₂ (Wall-Palmer et al., 2012, 2013; Manno et al., 2017). Single-season, in situ studies have shown correlations between carbonate chemistry conditions and pteropod shell dissolution, oxidative stress, relative abundance, and vertical distribution (Bednarski et al., 2012, 2014, 2017, 2018; Bednarski and Oehman, 2015; Feely et al., 2016; Engström-Öst et al., 2019). Observations of shell dissolution along natural gradients in aragonite saturation state (Ω₉₈) and snapshots of current pteropod distributions correlated with Ω₉₈ have been combined with historical reconstructions of carbonate chemistry to provide hypotheses about recent changes in pteropod abundance due to
OA (Bednarik et al., 2017). While spatial gradient studies show correlations with carbonate chemistry that provide strong evidence for a negative effect of OA on pteropod shell condition, they do not necessarily offer direct evidence of modern OA effects because they substitute space for time and make inferences about historical states without direct observations (McElhany, 2017). Available time-series analyses find no significant relationships between pteropod abundance and carbonate chemistry (Howes et al., 2015; Thibodeau et al., 2018). Recent analyses of pteropod abundance time-series from around the globe show that populations vary in trajectories with some declining, some increasing, and others showing no change; this is counter to what would be expected if the negative effects of OA now dominate population processes, suggesting that other local and regional drivers, including ocean warming, currently influence pteropods more than OA (Ohman et al., 2009; Head and Pepin, 2010; Mackas and Galbrath, 2012; Beare et al., 2013; Beaugrand et al., 2013). While both historical and modern samples suggest that pteropods are sensitive to carbonate chemistry conditions, more evidence is needed to link the progress of OA to impacts on the demographics of pteropod populations. It is possible that there are variable responses of pteropods in situ, time-series are not yet long enough to detect a directional change caused by OA, and/or the chemical thresholds at which ocean carbonate chemistry influences pteropods have not yet been crossed at the ecosystem scale.

Oysters
Impacts of elevated CO2 on oyster larvae were key in raising concerns about the implications of OA for marine ecosystems (Kelly et al., 2014). Laboratory studies have yielded a more complete understanding of the sensitivity of oysters to acidified conditions, documenting effects in the larval stage such as decreased calcification, reduced growth, delayed metamorphosis, and increased mortality (Miller et al., 2009; Talmage and Gobler, 2009; Watson et al., 2009; Parker et al., 2010, 2011; Dickinson et al., 2012; Waldbusser et al., 2013; Barton et al., 2015; Frieder et al., 2017). Laboratory research has also indicated that juvenile and adult oysters are sensitive to OA, though responses are variable. Some species and populations show changes in metabolism, calcification, and shell strength under OA conditions, with effects on juveniles sometimes carried over from larval exposure (Gazeau et al., 2007; Beniash et al., 2010; Welladsen et al., 2010; Parker et al., 2011, 2012; Hettinger et al., 2012; Sanford et al., 2014; Wright et al., 2014).

Carbonate chemistry conditions documented in shellfish hatcheries provide an example of how acidification can be linked to declines in larval performance in an artificial system (Barton et al., 2012; Ellis et al., 2017). Many oyster hatcheries now control seawater conditions (modification of carbonate chemistry, abundance of food, decrease in predation) and oyster producers have long practiced selection/breeding for performance (Barton et al., 2012; Ellis et al., 2017). Curiously, Pacific oyster recruitment still occurs in wild populations exposed to Ωar near threshold limits for calcification found in the laboratory (Ruesink et al., 2018). This apparent contradiction suggests that the influence of carbonate chemistry on oyster populations is complex and likely affected by varying and heterogeneous chemical conditions, other environmental factors, adaptation mechanisms, and/or transgenerational effects (Parker et al., 2010, 2012, 2017a, b; Dickinson et al., 2012; Hettinger et al., 2013; Ruesink et al., 2018). There is limited information about the micro-habitat carbonate chemistry conditions that natural oyster populations experience (Hales et al., 2017), though first principles suggest that they persist in a wide range of conditions given the influence of fluctuations in freshwater inputs, other dynamic physical drivers, and biological activity in their habitat. Over the last 130 years, a global decline in oyster populations has been driven by over-harvesting, competition with non-native species, disease, and other anthropogenic factors (Beck et al., 2011). Any role of OA in these changes in situ is still unclear due to the lack of available demographic data and related carbonate chemistry time-series in coastal environments.

Tropical coral reefs
The expectation that OA will negatively affect tropical coral reef calcification is rooted in thermodynamics (e.g. Plummer and Busenberg, 1987) and early abiogenic CaCO3 precipitation experiments that provided a quantitative framework within which to understand, predict, and interpret biological responses (Burton and Walter, 1987; Morse and Mackenzie, 1990). Subsequent experiments supported the prediction that as Ωar declines, calcification decreases (Langdon et al., 2000; Leclercq et al., 2002; Langdon and Atkinson, 2005) and CaCO3 dissolution increases (Andersson et al., 2007; Andersson and Gledhill, 2013). Field and laboratory-based studies suggest that OA may enhance the bioerosion capabilities of borers, increasing breakdown of the calcium carbonate framework (Tribollet et al., 2009; Wisshak et al., 2012; Silbiger et al., 2014; DeCarlo et al., 2015). Field studies have found correlations between Ωar and net ecosystem calcification (NEC), the net balance of gross ecosystem calcification and dissolution. For example, manipulative short-term, in situ, pulse alkalinization (Albright et al., 2016) and pulse acidification (Albright et al., 2018) experiments across a coral reef flat documented increased and decreased NEC, respectively, providing critical information for how net calcification responds to OA at the ecosystem level. Field observations across natural Ωar gradients report declines in coral skeletal density, coral diversity, colony size, NEC, and increases in bioerosion and dissolution with declining Ωar (Silverman et al., 2007; Manzello et al., 2008; Fabricius et al., 2011; Shamberger et al., 2011; Enochs et al., 2016; Silbiger et al., 2016; Eyre et al., 2018; Mollica et al., 2018). However, there are notable exceptions (e.g. Shamberger et al., 2014; Barkley et al., 2015; DeCarlo et al., 2017; Silbiger et al., 2017).

The general expectation, based on theoretical predictions and experimental results, is that OA should have already negatively affected coral reefs (Table 1). However, the current inability to confidently isolate and attribute effects of anthropogenic OA on coral reefs in situ suggests that either the current measurement methods are not sensitive enough to detect expected impacts, or these impacts have been mitigated by other processes or masked by varying oceanic changes that have stronger effects. Key insights from the last decade of OA coral reef studies are as follows:

- The metabolism of coral reef organisms strongly affects coral reef seawater chemistry (e.g. Shaw et al., 2012; Cyronak et al., 2014; Shamberger et al., 2014; DeCarlo et al., 2017) and may slow or enhance the acidification of the surrounding open-ocean source water to the reef.
- Corals and other coral reef organisms modulate the chemistry of their calcifying fluids and may override changes in the chemistry of the seawater source to the site of calcification.
(Cohen and Holcomb, 2009; Cohen et al., 2009; McCulloch et al., 2012).

- Coral feeding, availability of dissolved inorganic nutrients, and energetic demands related to reproductive status can mitigate or exacerbate the impact of OA on coral calcification (Langdon and Atkinson, 2005; Cohen and Holcomb, 2009; Holcomb et al., 2010; Edmunds, 2011; Drenkard et al., 2013; Silbiger et al., 2018; Kealoha et al., 2019).

- Ocean-warming-induced coral bleaching is an important dominant driver of declines in coral growth over the 20th century (Cantin et al., 2010; Courtney et al., 2017; Hughes et al., 2018) that may mask the influence of OA on coral growth histories. Naturally high variability and uncertainty in NEC measurements (Courtney and Andersson, 2019) makes it difficult to determine whether changes in NEC are driven by environmental change or are within the natural variability of the system (Silverman et al., 2014; Shamberger et al., 2018). One consistent response of coral reef organisms and ecosystems across natural gradients in pH, in both laboratory and field experiments and observations, is an increase in bioerosion and sediment dissolution (e.g. Barkley et al., 2015; DeCarlo et al., 2015; Silbiger and Donahue, 2015; Enochs et al., 2016; Silbiger et al., 2016; Eyre et al., 2018). However, these processes are also influenced by factors such as nutrient inputs and organic matter content of sediments, and deconvolving the various contributions remains challenging.

### Research needs for OA attribution in biological systems

Great strides have been made to understand OA impacts. In this perspective, we highlight that laboratory-based studies have identified a variety of ways that a broad taxonomic range of marine species are sensitive to elevated CO₂. Informed by these experimental results, progress is also being made on the detection and attribution of anthropogenic OA impacts in wild populations (Table 1). For example, some biological impacts in situ have been correlated with carbonate chemistry and suggest attribution to OA, such as decreased shell dissolution of pteropods (Bednaršek et al., 2014) and decreased shell thickness in planktic foraminifera (de Moel et al., 2009; Moy et al., 2009; Fox et al., 2020; Osborne et al., 2020). However, impacts attributable to OA have yet to be detected on ecosystem-level biological parameters such as population density, trophic interactions, or energy transfer through food webs. To improve our detection and attribution ability, research is needed to determine impacts of OA in situ. For some taxa, like oysters, studies are needed to understand how OA may influence the entire life cycle, since OA has different effects across life stages (Pandori and Sorte, 2019). Other groups discussed (seagrasses, oysters, and coral reefs) require efforts to tease out the influence of OA from other co-varying factors that drive physical and chemical conditions (Table 1). Below, we detail four avenues of research that would improve the ability to detect and attribute impacts of OA on marine ecosystems in situ.

### Summary of marine system responses to OA

| Marine groups          | Summary of experimental findings | Observations of wild populations | Data/analysis that could increase detection in situ |
|------------------------|----------------------------------|---------------------------------|----------------------------------------------------|
| Seagrasses             | Increased productivity, shoot density, and biomass; changes in community composition | No effects attributable directly to OA | Improved understanding of the interplay of the factors that drive seagrass abundance and distribution |
| Pteropods              | Dissolution, reduced calcification, physiological and early life stage impairments, mortality | Dissolution in naturally low pH environments; no population effects attributable directly to OA | Multi-factor analyses to tease out the role of OA in driving pteropod condition and population dynamics from modern and historical samples |
| Oysters                | Reduced calcification/growth, physiological effects, and mortality, particularly in larvae and juveniles | No effects attributable directly to OA | Condition and demography of populations living in different carbonate chemistry environments; studies of the effects of OA throughout the entire life cycle in the context of multiple interacting drivers |
| Coral reef ecosystems  | Reduced calcification, increased dissolution, and bioerosion | Increased bioerosion and dissolution; no effects attributable directly to OA | Constrain natural spatiotemporal variability of NEC; understand response to multiple interacting drivers; long-term time-series studies of environmental and reef conditions |

The expected impacts are based on laboratory/mesocosm CO₂ sensitivity experiments, and observations are based on in situ studies (e.g. time-series, natural pH gradients). Data or analyses that may improve the probability of detecting the impacts of OA in situ are suggested.
anthropogenic input of CO₂ (Gruber et al., 1996; Feely et al., 2016; Carter et al., 2017). These statistical methods will aid in quantifying chemical changes in the oceans due to OA and linking biological impacts. Global coordination of OA monitoring through the Global Ocean Acidification Observing Network will aid robust data collection and synthesis needed for estimating anthropogenic input of CO₂ (Newton et al., 2019; Tilbrook et al., 2019).

(2) Attribute biological impacts to OA among other co-varying parameters: marine organisms face multiple changing and co-varying physical and chemical parameters associated with climate change (e.g. OA, warming, hypoxia). Identifying specific biological traits that can be measured in situ and empirically linked to OA impacts is of crucial importance in advancing efforts to detect in situ impacts of OA. Such traits of interest to monitor in situ can be physiological (Strader et al., 2019), structural [e.g. coral skeletal density changes in Mollica et al. (2018); foraminifera test thickness changes in Moy et al. (2009)], or components of population fitness (Falkenberg et al., 2018). Importantly, there is a great need to understand how differential sensitivities to OA exist within a species’ life cycle (Byrne and Przeslawski, 2013). In addition, increased efforts to monitor community-level traits of interests (e.g. population density, biomass) are needed to understand ecological alterations in marine ecosystems due to OA. With all research techniques, a holistic approach of detailed characterization of both biological impacts in conjunction with physical and chemical environmental parameters are needed to achieve such an aim.

(3) Understand how ecological-evolutionary dynamics alter OA responses in situ: feedbacks between changing conditions in marine environments and organismal adaptation potential have been highlighted with recent efforts to understand the interplay between ecology and evolution (eco–evo dynamics) in driving demographic responses (Parmesan, 2006; Chevin et al., 2013). These eco–evo dynamics on longer time scales have the potential to facilitate intra-generational adaptation to changing ocean conditions through the interplay of ecological processes such as range shifts (Sunday et al., 2012; Vergès et al., 2014; Pecl et al., 2017), alteration in phenotype such as a modification of microbiome (Botté et al., 2019), as well as epigenetic mechanisms (Putnam et al., 2016; Hofmann, 2017). It is crucial to understand how OA has the potential to alter plasticity of phenotypes, which in turn could either constrain adaptive genetic changes through the persistence of diverse genotypes within the population or promote adaptive genetic changes through allowing for persistence in extreme environments (Hendry, 2016). Phytoplankton, in particular, have been used to test the hypothesis that increased phenotypic plasticity over multiple generations will lead to increased evolution in OA conditions (Collins, 2011; Lobbeck et al., 2012; Schaum and Collins, 2014) and have found increased plasticity as a good indicator of adaptation to increasing CO₂ conditions (Schaum and Collins, 2014). Future research could expand on current studies that focus on understanding phenotypic plasticity of organismal physiology (Torda et al., 2017; Donelson et al., 2018; Ryu et al., 2018; Willoughby et al., 2018; Catullo et al., 2019) by using modelling efforts that incorporate eco–evo dynamics of both past and future OA conditions.

(4) Characterize ecosystem trajectories through long-term monitoring: understanding how and why species are sensitive to OA has vastly improved, but this is just one aspect of understanding population and ecosystem responses in situ. For example, a species’ population dynamics may be influenced more by OA-induced modifications of ecological interactions than by direct sensitivity (Marshall et al., 2017). In some instances, ecological interactions have been hypothesized to mitigate OA impacts through enhancing adaptive capacity or mitigating the effects of elevated CO₂ conditions (Kapsenberg and Cyronak, 2019). To attribute changes in species dynamics or ecological processes to OA, more work is needed to describe how OA impacts scale in space and time. Insights into ecosystem environmental changes can be gained using shell geochemistry as paleo-proxies to document OA effects (Foster and Rae, 2016), and potentially how further changes in ocean conditions are linked to mass extinction and declines in biodiversity (Kessling and Simpson, 2011; Hemmige et al., 2014). Modelling exercises can help elucidate ecological processes, but they cannot replace time-series biological data. Of particular importance are long-term observational studies that pair a detectable chemical signal of OA with biological responses that account for ecological processes and patterns (e.g. yearly population growth patterns, NEC). With detailed datasets, broad comparative trends can be used to understand mechanisms of resilience to disturbance events. For example, comparative data indicate that community resilience to changing conditions can develop from various environmental drivers such as indiscriminate disturbance events of crown-of-thorns starfish in Mō’orea, French Polynesia, and repeated thermal stress in Panama, Eastern Tropical Pacific (Edmunds et al., 2019). The variation in environmental drivers has resulted in differences in reproductive strategies of dominant reef-building corals, coral-algal symbiotic communities, functional diversity of herbivorous fishes, and the reef framework (Edmunds et al., 2019), highlighting that comparative approaches can be used to understand how differing environmental drivers (such as OA) can alter ecosystem trajectories.

Current challenges in attributing large-scale OA effects on marine systems does not mean that there has been no OA effect to date nor that there will not be one in the future. We are beginning efforts to detect and attribute OA impacts in situ, with experimental results informing field campaigns and observational studies approaching the time of emergence for an OA signal in increasingly variable environments. Knowledge accumulated over the last decade puts us in a better position to design an observation system that could detect the emergence of impacts of OA at species and ecosystem levels. Research on species sensitivity to OA that can be scaled into projected ecosystem-level impacts in a multi-stressor ocean and verified with in situ detection is critical to inform the conservation and sustainable use of ocean ecosystems.

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Author contributions
All authors conceived the idea for this paper in discussion at a workshop and contributed to the writing of the manuscript. SSD and DSB led the group and contributed the most to the text.

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