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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 CO_2 in coastal and open-ocean waters to understand how this increase in CO_2 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 CO_2 contribution, coral reefs, ecological-evolutionary dynamics, ecosystem trajectory, oysters, pteropods, seagrass

Introduction

A third of the anthropogenic CO_2 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 CO_2 conditions. Controlled experiments have found relationships between organism responses and CO_2 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 CO_2 (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-Muñiz *et al.*, 2017; Riebesell *et al.*, 2017, 2018). Field-based observations are largely gleaned from natural CO_2 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 CO_2 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 CO_2 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 CO_2 (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; Andersson *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 CO_2 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 CO_2. 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 CO_2. 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 CO_2 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.

Seagrass

Seagrasses are commonly considered potential beneficiaries of OA; they are carbon-limited under current CO_2 conditions and increase photosynthesis under higher CO_2 concentrations (Koch *et al.*, 2013). This is in contrast to most marine autotrophs, which have developed efficient strategies for utilizing bicarbonate (HCO_3^-), and is due to the relatively recent evolution of marine seagrasses under comparatively higher CO_2 concentrations (Beer and Koch, 1996; Zimmerman *et al.*, 1997). Results from mesocosm and *in situ* manipulations of CO_2 indicate increased seagrass productivity, shoot density, and biomass under elevated CO_2 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 CO_2 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 CO_2. 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 CO_2 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 CO_2 during the day, potentially equal or greater night-time respiration may counteract daytime effects by increasing CO_2, 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 CO_2 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 CO_2, 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 CO_2 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 CO_2 (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 (Bednaršek *et al.*, 2012, 2014, 2017, 2018; Bednaršek and Ohman, 2015; Feely *et al.*, 2016; Engström-Öst *et al.*, 2019). Observations of shell dissolution along natural gradients in aragonite saturation state (Ω_{ar}) and snapshots of current pteropod distributions correlated with Ω_{ar} have been combined with historical reconstructions of carbonate chemistry to provide hypotheses about recent changes in pteropod abundance due to

OA (Bednaršek *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 Galbraith, 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 CO_2 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 Ω_{ar} 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 $CaCO_3$ 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 Ω_{ar} declines, calcification decreases (Langdon *et al.*, 2000; Leclercq *et al.*, 2002; Langdon and Atkinson, 2005) and $CaCO_3$ 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 Ω_{ar} 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 Ω_{ar} gradients report declines in coral skeletal density, coral diversity, colony size, NEC, and increases in bioerosion and dissolution with declining Ω_{ar} (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 co-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

Table 1. 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 CO_2 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.

(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 CO_2. 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 increased 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*.

(1) Quantify the anthropogenic contribution of CO_2 in coastal environments: a challenge for attributing change in biological systems to OA is knowledge of the chemical conditions that a species or community inhabits and how OA has altered them. The majority of long-term ocean pH/pCO_2 measurements have been made in the open-ocean, which is relatively stable chemically. Coastal oceans tend to have shorter time-series measurements of pH/pCO_2, complex biogeochemical and physical processes, and a higher rate of biological activity, causing larger diel, seasonal, and episodic fluctuations in ocean chemistry (e.g. Hofmann *et al.*, 2011; Guadayol *et al.*, 2014; Chan *et al.*, 2017; Silbiger and Sorte, 2018; Lowe *et al.*, 2019). While the chemical signal of OA has already emerged in open oceans, it will take longer to emerge in coastal ecosystems (Sutton *et al.*, 2019). Therefore, we suggest further studies that employ statistical methods to estimate

anthropogenic input of CO_2 (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 CO_2 (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; Vergés *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; Lohbeck *et al.*, 2012; Schaum and Collins, 2014) and have found increased plasticity as a good indicator of adaptation to increasing CO_2 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 CO_2 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 situ* 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 (Kiessling and Simpson, 2011; Hennige *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 Mo'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 symbiont 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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