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Ocean acidification refugia in variable environments

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Abstract

Climate change refugia in the terrestrial biosphere are areas where species are protected from global environmental change and arise from natural heterogeneity in landscapes and climate. Within the marine realm, ocean acidification, or the global decline in seawater pH, remains a pervasive threat to organisms and ecosystems. Natural variability in seawater carbon dioxide (CO_2) chemistry, however, presents an opportunity to identify ocean acidification refugia (OAR) for marine species. Here, we review the literature to examine the impacts of variable CO_2 chemistry on biological responses to ocean acidification and develop a framework of definitions and criteria that connects current OAR research to management goals. Under the concept of managing vulnerability, the most likely mechanisms by which OAR can mitigate ocean acidification impacts are by reducing exposure to harmful

conditions or enhancing adaptive capacity. While local management options such as OAR show some promise, they present unique challenges and reducing global anthropogenic CO_2 emissions must remain a priority.

Introduction

Climate change refugia are areas where localized environmental conditions protect species from the unfavorable or harmful conditions associated with broad transformations of Earth's climate (Ashcroft, 2010, Keppel *et al.*, 2012, Morelli *et al.*, 2016). *A priori* knowledge of anthropogenic climate change trajectories and biological impacts provides opportunities to identify climate change refugia and invest in local management actions. The oceans play a critical role in regulating Earth's climate, are of enormous socio-economical value, and are disproportionally affected by climate change (IPCC, 2014). The three main climate change phenomena expected to impact many marine ecosystems are warming, sea level rise, and ocean acidification (Doney *et al.*, 2012, Gattuso *et al.*, 2015, Hoegh-Guldberg & Bruno, 2010, Poloczanska *et al.*, 2013). Ocean acidification refers to the global changes in seawater carbon dioxide (CO_2) chemistry associated with the absorption of anthropogenic CO_2 emissions (Doney *et al.*, 2009), which results in increases in pCO_2 and $[HCO_3^-]$ and decreases in pH and calcium carbonate saturation state (Ω) (Zeebe & Wolf-Gladrow, 2001). These changes in CO_2 chemistry have the potential to negatively affect many marine organisms and ecosystems (Kroeker *et al.*, 2013, Pörtner *et al.*, 2014) and alter the global carbon cycle for millennia to come (Caldeira & Wickett, 2003, Hönisch *et al.*, 2012). By protecting sensitive species and ecosystems, refugia could help maintain valuable marine resources and services upon which our society depends (Billé *et al.*, 2013, Gattuso *et al.*, 2015, Gattuso *et al.*, 2018, McLeod *et al.*, 2013).

How and where to invest in ocean acidification management efforts, including the identification of refugia, remains largely unresolved (Albright *et al.*, 2016, Billé *et al.*, 2013, Gattuso *et al.*, 2018), in part due to the complexity of seawater CO_2 chemistry in marine waters (Bates *et al.*, 2018, Hurd *et al.*, 2018, Strong *et al.*, 2014). Much like weather and climate on land, seawater conditions vary dramatically over hours to seasons (Waldbusser & Salisbury, 2014). *Ocean weather* can be thought of as the state of seawater chemistry, temperature, currents, etc. in a location at any given moment in time (Bates *et al.*, 2018). *Ocean climate*, on the other hand, can be thought of as the average chemical and physical seawater conditions across regions, while small-scale differences within a climatology can create restricted areas that encapsulate *ocean microclimates*. Global surface ocean pH climatologies naturally range between pH 8.0-8.2 (Bates *et al.*, 2014) and are predicted to decline by >0.4 units if CO_2 emissions continue at the current rate (Pörtner *et al.*, 2014). Locally, however, marine ecosystems exhibit seawater acidification rates that differ from what is expected based on atmospheric CO_2 forcing alone (Cai *et al.*, 2011, Cyronak *et al.*, 2014b, Feely *et al.*, 2010, Kapsenberg *et al.*, 2017a, Provoost *et al.*, 2010, Wootton *et al.*, 2008). This is because many biogeochemical and physical drivers influence local seawater CO_2 chemistry (Fig. 1, Box 1) and may themselves be influenced by changes to Earth's climate (*e.g.,* temperature, precipitation, upwelling). Natural variability and interaction of these drivers generates unique variations in seawater CO_2 chemistry across marine ecosystems (Chan *et al.*, 2017, Duarte *et al.*, 2013, Hofmann *et al.*, 2011, Waldbusser & Salisbury, 2014), such that marine species, and distinct populations, are likely to encounter different future trajectories depending on their location and habitat (Jury *et al.*, 2013, Kapsenberg *et al.*, 2015, Kwiatkowski & Orr, 2018, Landschützer *et al.*, 2018, Pacella *et al.*, 2018, Shaw *et al.*, 2013).

The presence of spatial and temporal variability in CO_2 chemistry across marine ecosystems has recently raised the idea that ocean acidification refugia (OAR), or locations where ocean acidification impacts could be less intense, exist naturally (Manzello *et al.*, 2012). Proposed OAR include seagrass meadows and dense algal beds (Hendriks *et al.*, 2014, Krause-Jensen *et al.*, 2015, Manzello *et al.*, 2012, Unsworth *et al.*, 2012, Wahl *et al.*, 2018, Young & Gobler, 2018), algal boundary layers (Cornwall *et al.*, 2014, Hendriks *et al.*, 2017, Noisette & Hurd, 2018), mangroves (Sippo *et al.*, 2016, Yates *et al.*, 2014), slow-flow habitats (Hurd, 2015), deep-sea mounts (Tittensor *et al.*, 2010), areas isolated from upwelling (Chan *et al.*, 2017, Kapsenberg & Hofmann, 2016), and productive high latitude environments (Hendriks *et al.*, 2017, Krause-Jensen *et al.*, 2016). These examples vary dramatically across spatial scales (*e.g.,* a few millimeters in an algal boundary layer to a 100 m^2 seagrass bed), with no clear criteria as to what makes each area a potential OAR other than observed transient increases in seawater pH relative to surrounding waters. The lack of a clear, agreed-upon definition for OAR and criteria for how they must function in the context of climate change makes it difficult for managers, legislators, and scientists to assess where to invest management efforts. In this perspective, we critically evaluate the concept of OAR in the context of organismal exposures to variable CO_2 chemistry and propose target refugia for research and management.

Defining Ocean Acidification Refugia

To build a framework for OAR, we turned to the recent interest in phytoremediation as a means for the local mitigation of ocean acidification through photosynthesis (Washington State Blue Ribbon Panel on Ocean Acidification, 2012, Nielsen *et al.*, 2018). Unlike many other global change stressors, the intensity of ocean acidification exposures is directly modified by the metabolism of marine organisms (*e.g.,* respiration and/or photosynthesis), which can add or remove CO_2. For example, daytime photosynthesis by seagrass meadows can radically elevate seawater pH across spatial scales of a few millimeters to hundreds of meters (Guilini *et al.*, 2017, Hendriks *et al.*, 2014, Manzello *et al.*, 2012). For this reason, the idea of seagrass ecosystems, and phytoremediation in general, acting as OAR has garnered considerable attention within the scientific community (Hendriks *et al.*, 2014, Manzello *et al.*, 2012, Young & Gobler, 2018), governments (Washington State Blue Ribbon Panel on Ocean Acidification, 2012, Nielsen *et al.*, 2018), and the media (OA-ICC, 2018). One issue with the concept of seagrass ecosystems acting as OAR is that times of net photosynthesis are accompanied by periods of net respiration on daily and seasonal timescales (Duarte *et al.*, 2010, Unsworth *et al.*, 2012). Therefore, any benefits of periodic relief from ocean acidification exposures due to pH increases during times of net seagrass photosynthesis (*e.g.,* Semesi *et al.*, 2009) must be critically evaluated against any potential harmful effects due to intensifying exposures that occur in these habitats during times of net respiration (Cyronak *et al.*, 2018, Pacella *et al.*, 2018, Unsworth *et al.*, 2012). Furthermore, the CO_2 chemistry in seagrass habitats is influenced by other biogeochemical and physical processes that act over timescales ranging from hours to seasons (Box 1) (Duarte *et al.*, 2013). Consequently, the presence of seagrass alone does not guarantee reduced exposure to harmful conditions (Cyronak *et al.*, 2018, Koweek *et al.*, 2018), nor does it necessarily translate to a biological benefit (Greiner *et al.*, 2018). This disconnect between seawater chemistry and biological impacts highlights the need to create a defining set of criteria that will allow the scientific and management communities to critically evaluate the effectiveness of potential OAR.

We define **Ocean Acidification Refugia** *as any area of the coastal or open ocean that exhibits persistent environmental conditions such that a species' vulnerability to anthropogenic ocean acidification is reduced, where vulnerability is the combination of* *sensitivity, exposure, and adaptive capacity* (Dawson *et al.*, 2011, McLeod *et al.*, 2013, Williams *et al.*, 2008). Inherent to this definition is that the local environmental conditions that define the refugium must, (1) provide a significant biological benefit, and, (2) persist through time, such that a species can outlast anthropogenic ocean acidification across generations. Based on the definition of climate change refugia by Morelli *et al.* (2016), we reiterate that the size of a refugium must be large enough to manage a small (meta)population. Therefore, we do not consider potential micro-refugia wherein seawater chemistry is modified within the boundary layers of photosynthesizing organisms (Flynn *et al.*, 2012, Hendriks *et al.*, 2017, Noisette & Hurd, 2018), even though this could benefit small epiphyte communities (Cox *et al.*, 2017).

Our definition of OAR purposefully allows for environmental factors other than seawater CO_2 chemistry to mitigate the harmful impacts of ocean acidification. For example, food supply has been shown to reduce species sensitivity to ocean acidification (Ramajo *et al.*, 2016). In some cases, environmental or ecological interactions, such as competition for light or space, might be more important in driving biological responses rather than CO_2 exposures (Barry *et al.*, 2013, Connell *et al.*, 2017, Garrard *et al.*, 2014). However, as natural variability in seawater CO_2 chemistry ultimately drives the severity of ocean acidification exposure and is expected to increase in the future (*e.g.,* Flynn *et al.*, 2012, Jury *et al.*, 2013, Pacella *et al.*, 2018, Shaw *et al.*, 2013), we focus this perspective on the biological impacts of exposure to variable CO_2 chemistry. The ocean acidification research community has, over the last few years, made significant progress on this topic (Fig. S1) (Boyd *et al.*, 2016, Hurd *et al.*, 2018, Rivest *et al.*, 2017), and the emerging trends could help inform target refugia and management strategies.

Biological Impacts of Variable CO_2 Chemistry

Throughout this paper, we use the term ‘variable CO_2 chemistry’ to refer to spatial and temporal changes in the seawater carbon dioxide system (*e.g., p*CO_2, pH, [HCO_3^-], Ω, see Box 1). In order to examine how variable CO_2 chemistry influences the effectiveness of OAR, we reviewed all studies published through 2018 that assessed the impact of natural CO_2 variability on marine species in the context of ocean acidification (*see* Supplemental Material for details). Across a total of 61 studies (Fig. S1, Table S1) and 172 observed biological responses, 62% of biological responses exhibited no sensitivity to variability treatments. These studies, however, can be divided into two categories: *environmental history* or *direct exposure*, and have different implications for the assessment of OAR.

Environmental history studies used the CO_2 variability observed in an organisms’ habitat to interpret their sensitivity to ocean acidification at a species level. Organisms of the same species, or closely related species, were collected from at least two sites with contrasting variability regimes and were exposed to elevated and stable CO_2 conditions simulating future ocean acidification. Environmental history comparisons tested the hypothesis that long-term exposure (≥ one generation) to variable CO_2 conditions enhances the physiological tolerance of populations to ocean acidification. These studies provide information on sensitivity, adaptive capacity, and the potential for evolution on timescales greater than one generation (Dawson *et al.*, 2011, Kelly & Hofmann, 2013, Williams *et al.*, 2008). Studies testing an organism’s environmental history demonstrated a positive effect of variability in 47% of the observations, with few observed negative effects (7%, Fig. 2a).

The *direct exposure* approach used experimental treatments wherein organisms were exposed to varying CO_2 conditions directly (*e.g.,* growing organisms under stable and fluctuating CO_2 conditions with present-day and future mean pH conditions). In contrast to the environmental history approach, direct exposure studies used organisms collected from a single population and tested the hypothesis that biological sensitivity to ocean acidification is altered when the organism is directly exposed to fluctuating conditions under simulated ocean acidification. Such studies provide insight on sensitivity to ocean acidification in the context of local environmental variability. In studies testing direct exposures, a near-equal and low percentage of positive (16%) and negative (14%) effects were observed (Fig. 2a).

Combined, these results indicate that an organism's long-term (at least one generation) exposure to harmful conditions has some potential to boost adaptive capacity to ocean acidification, while direct exposure to variability will, in the majority of cases, not alter biological responses. When direct exposure to variability did alter ocean acidification sensitivity, the responses were highly mixed across organisms and biological processes (Fig. S2-3). Therefore, it is not expected that direct effects of variability will influence biological responses to ocean acidification as much as changes in mean conditions will.

To further explore these trends, we grouped organisms into 4 categories based on their mode of life (photosynthesizing, calcifying, both, or neither). In environmental history studies, non-photosynthesizing calcifiers (NP-C) exhibited an overwhelmingly positive effect, wherein a variable environmental history reduced sensitivity to ocean acidification in 76% of observed biological responses (Fig. 2b). Organisms in this category consisted of echinoderms, mollusks, crustaceans, and bryozoans and were predominantly collected from temperate upwelling or riverine-influenced sites. Echinoderms were the most studied taxa within the environmental history approach (7 papers), with consistent independent observations across species, regions, habitats, and life stages. For example, sea urchin fertilization exhibited increased ocean acidification tolerance associated with CO_2 variability in tidepools and upwelling habitats (Kapsenberg *et al.*, 2017b, Moulin *et al.*, 2011). Likewise, sea urchin larval growth exhibited reduced ocean acidification sensitivity when parents originated from sites with high and variable CO_2 levels (Gaitán-Espitia *et al.*, 2017, Kelly *et al.*, 2013). Similar observations have been made for mollusks, where differences in sensitivities to ocean acidification were correlated to CO_2 exposure history (Thomsen *et al.*, 2017, Vargas *et al.*, 2017). Food supply and nutritional status likely play into population-specific pH sensitivities, but sites of high pH variability with frequent low pH events are not always coupled to high food supply (Kroeker *et al.*, 2016). Taken together, these results provide strong evidence that exposure to CO_2 variability has the potential to modulate non-photosynthesizing calcifiers' sensitivity to ocean acidification and enhance their adaptive capacity (Kelly & Hofmann, 2013).

The observed benefit of variable CO_2 history for NP-C type organisms is in stark contrast to photosynthesizing-calcifiers (P-C). The P-C group, comprised mostly of temperate and tropical corals and coralline algae, largely exhibited indifference to variability (81% no effect), with a near equal and low number of positive and negative effects (Fig. 2b). It may be that P-C organisms are less influenced by CO_2 variability at the habitat scale due to acclimation to large daily CO_2 fluctuations that, depending on flow regimes, can occur within their diffusive boundary layers due to the interactive effects of photosynthesis, respiration, and calcification (Gattuso *et al.*, 1999, Hurd *et al.*, 2011). The contrasting responses to ocean acidification sensitivity based on environmental history across different modes of life (*i.e.,* NP-C compared to P-C) highlights the need to develop a better mechanistic understanding of how CO_2 chemistry is regulated at the cellular level and how changes in environmental conditions alter biological processes.

Contrary to environmental history studies, when organisms were directly exposed to variable CO_2 chemistry, no mode of life showed an obvious advantage or disadvantage under simulated ocean acidification (Fig. 2c). Direct effects were few ($N \leq 10$, combined positive and negative), with the vast majority of biological processes unresponsive to fluctuating CO_2 conditions. This indicates that transient increases in pH are unlikely to protect organisms from ocean acidification if there are also transient decreases in pH, especially if the mean pH is no different from the mean pH of the source waters (although there may be exceptions, *e.g.,* Jarrold *et al.*, 2017).

Based on this literature review, we can make three broad conclusions. First, in the majority of observations, directly exposing marine organisms to short-term fluctuations in CO_2 chemistry (*e.g.,* hours) does not appear to modulate their biological response to ocean acidification. Therefore, to mitigate ocean acidification impacts via reduced exposures, a substantial increase in mean pH will be necessary independent of local variability regimes. Second, exposure to variable CO_2 conditions over the course of at least one generation may expand a species' adaptive capacity and CO_2 tolerance window. Currently, this effect is most apparent in NP-C organisms from temperate environments. Third, while few, the presence of both positive and negative effects of CO_2 variability indicate that ocean acidification impacts could vary from predicted responses in dynamic environments (Fig. S2-3).

Ocean Acidification Refugia Management

Our best hope for maintaining biodiversity in a changing climate is by exploiting natural variations in vulnerability, defined as the combination of a species sensitivity, exposure, and adaptive capacity (Dawson *et al.*, 2011, Williams *et al.*, 2008). In this vein, recent proposed ocean management strategies consider management of both environmental exposures, such as reducing CO_2 emissions, and biological responses, such as ecosystem restoration or assisted evolution, as potential solutions to mitigate climate change impacts (Gattuso *et al.*, 2018). For ocean acidification impacts, most biological responses were unchanged in the presence of temporal variability in CO_2 chemistry (Fig. 2c), indicating that responses to mean changes in environmental conditions remain highly relevant (Kroeker *et al.*, 2013). Therefore, temporary pH increases without a substantial change in mean pH (*e.g.,* pH increases associated with primary production over tidal or diel cycles) should not be an identifying criterion for OAR, and reducing global CO_2 emissions must remain the primary management activity (Gattuso *et al.*, 2015). However, exposure to variability in CO_2 chemistry, specifically low pH events (*e.g.,* days to weeks of low pH exposure driven by upwelling), does seem to reduce vulnerability to ocean acidification by enhancing adaptive capacity. This was most consistently observed for non-photosynthesizing calcifiers (Fig. 2). Based on these results, OAR could help protect species from ocean acidification via one of two mechanisms: (1) modulating exposure to harmful conditions (*e.g.,* areas with sustained high mean pH), or, (2) enhancing adaptive capacity (*e.g.,* areas with frequent low pH exposures) (Box 2). Because OAR based on mitigating exposures require an increase in mean pH and OAR based on stimulating adaptive capacity require frequent low pH events, these two classes of OAR are mutually exclusive in terms of CO_2 variability regimes. However, other mechanisms that reduce a population's vulnerability to ocean acidification (*e.g.,* food supply) could potentially occur in either class of OAR.

Ocean acidification refugia based on mitigating exposures

Management of CO_2 chemistry exposure (Fig. 1) is currently the most common strategy for recently proposed OAR and falls under two categories: *spatial refugia* and *small-scale operative refugia* (Box 2). Based on our literature review and previous biological response studies (Kroeker *et al.*, 2013), any region with a sustained increase in mean seawater pH or that is consistently isolated from corrosive high CO_2 conditions has the potential to function as a *spatial refugium*, regardless of local CO_2 variability regimes. While *spatial refugia* are not isolated from ocean acidification *per se*, organisms living in these refugia will face better environmental conditions relative to their sister populations that encounter more corrosive conditions, whilst maintaining connectivity and the potential for genetic exchange. *Spatial refugia* based on physical characteristics are likely to persist through time. Examples include microclimates such as areas shielded from corrosive upwelling events (Chan *et al.*, 2017, Kapsenberg & Hofmann, 2016) and deep-sea mounts which isolate organisms from deeper CO_2-rich waters (Tittensor *et al.*, 2010). *Spatial refugia* based on the biological removal of CO_2 potentially exist in hotspots of primary production. For example, in high-latitude environments the extended photoperiod and high nutrient levels maintain primary production and high pH for several months in summer (Duarte & Krause-Jensen, 2018, Havenhand *et al.*, 2018, Kapsenberg *et al.*, 2015, Krause-Jensen *et al.*, 2016). Like other *spatial refugia*, high latitude environments are not isolated from ocean acidification and are actually considered one of the most vulnerable ecosystems due to naturally cold, CO_2-rich waters (Orr *et al.*, 2005). So far, we are unaware of studies that have tested the hypothesis that seasonally-restricted high pH benefits an organism’s sensitivity to ocean acidification. Nonetheless, primary production hotspots could function as *spatial refugia* if high pH levels are sustainable for a period of biological significance relative to areas with lower primary productivity.

Exposure can also be managed directly in *small-scale operative refugia* (Box 2). Purposeful modification of seawater CO_2 chemistry will be most feasible in easily accessible coastal locations and for target economic purposes, such as aquaculture or small-scale reef management (Mongin *et al.*, 2016). Phytoremediation, or modification of seawater CO_2 chemistry by seagrass, kelp, or algae cultivated alongside ocean acidification sensitive organisms is an active area of research (Young & Gobler, 2018). However, its effectiveness in the field has significant limitations (Greiner *et al.*, 2018, Mongin *et al.*, 2016), and additional bubble-stripping of high nighttime CO_2 levels in macrophyte beds may be necessary to ensure that the overall mean pH is significantly elevated to compared to that of surrounding waters (Koweek *et al.*, 2016). Nighttime bubbling with air may be particularly effective in slow flow environments where diel pH cycles can be large (Hurd, 2015). Even if a substantial increase in mean pH is achieved, use of marine vegetation as the basis of *small-scale operative refugia* must be evaluated in the context of seasonal changes in primary production (Duarte *et al.*, 2010, Unsworth *et al.*, 2012). Artificial ocean alkalization is another method currently under evaluation aimed at directly modifying exposures (Gattuso *et al.*, 2018, Ilyina *et al.*, 2013, Renforth & Henderson, 2017). Increasing total alkalinity may be achieved by adding crushed shells or concrete to key habitats, which then through dissolution causes an increase in seawater calcium carbonate saturation state (Green *et al.*, 2013, Green *et al.*, 2009, Greiner *et al.*, 2018, Mos *et al.*, 2019). The effectiveness of passive calcium carbonate dissolution in mitigating biological impacts in the field will be highly dependent on local hydrology and is potentially restricted to specific biological processes in small boundary layers or shallow sediments (Green *et al.*, 2013, Green *et al.*, 2009, Mos *et al.*, 2019).

Regardless of the exact method, management of *small-scale operative refugia* will require intense resource investment in the form of engineering, maintenance, restoration, monitoring, and funding. *A priori* knowledge of the local environment will be necessary to choose where to implement such efforts so that other coastal drivers, such as groundwater, terrestrial run-off, or high flow rates (Fig. 1) do not wash-away or neutralize the expected benefits of the management approach. Watershed inputs, including surface runoff, groundwater, excess nutrients and other materials, may need to be included in the management plan in order to achieve the management goals of the refugium. The long-term persistence of *small-scale operative refugia* will largely depend on the duration of resource investments. For phytoremediation specifically, additional management costs may be required to protect macrophytes from other climate change impacts such as marine heat waves (Arias-Ortiz *et al.*, 2018, Filbee-Dexter *et al.*, 2016). While purposeful local management of CO_2 chemistry to protect target marine resources, such as aquaculture or small reefs, could offer short-term benefits for a few years (Mongin *et al.*, 2016), OAR based on physical features (*e.g.,* some spatial refugia) may function for a much longer time period.

Ocean acidification refugia based on enhancing adaptive capacity

Intense variability in CO_2 chemistry, specifically exposure to frequent low pH events (*e.g.,* days to weeks), can enhance adaptive capacity, suggesting that OAR may also exist as *adaptive refugia* in 'exposure hotspots' (Chan *et al.*, 2017) (Box 2). Rather than managing exposures, *adaptive refugia* reduce a species' vulnerability to ocean acidification by enhancing their potential to adapt to changing conditions (Dawson *et al.*, 2011). Based on our literature review, enhancing adaptive capacity is currently the most likely means by which variable seawater CO_2 chemistry can mitigate ocean acidification impacts. So far, this appears most effective for NP-C type organisms in temperate ecosystems (Fig. 2b), although research for other biomes is lacking. Adaptive capacity can potentially accrue via changes in physiological plasticity, epigenetics, genetics, or a combination thereof (Hoffmann & Sgrò, 2011, Hofmann, 2017). The benefit of intermittent exposure to low pH, such as that associated with upwelling, is likely influenced by frequency and duration of the low pH events, generation time, and life history of the organism (Boyd *et al.*, 2016). For management, marine protected areas encompassing *adaptive refugia* could help protect and maximize the genetic diversity necessary for adaptation and dispersal thereof, while reducing other local stressors (Bernhardt & Leslie, 2013, Roberts *et al.*, 2017).

Like *spatial refugia*, *adaptive refugia* are not isolated from ocean acidification and local adaptation is unlikely to provide complete resistance to ocean acidification (Gaitán-Espitia *et al.*, 2017, Kelly *et al.*, 2013). The increasingly harmful low pH and calcium carbonate undersaturation associated with ocean acidification at exposure hotspots may ultimately challenge the persistence of a local population (Hauri *et al.*, 2009). Thus, *adaptive refugia* must last long enough to generate and disperse adaptive geno- or pheno-types elsewhere. This duration will be influenced by species-specific characteristics such as life history and rates of adaptation. Ideally, *adaptive refugia* should encompass source populations that disperse to *spatial refugia* where ocean acidification effects are less intense. Understanding population connectivity, and how it might be altered by global change, will be an important aspect of deciding where to invest climate change management efforts (Magris *et al.*, 2014, Palumbi, 2003). For example, resource investment at sites with sink populations, where the persistence of the population depends on immigration from reproductive populations elsewhere, could be futile. Ocean acidification itself could alter a species' ability to successfully disperse to new habitats. For example, the ability for larval clownfish to detect settlement cues is diminished under simulated ocean acidification (Munday *et al.,* 2009, but see also Jarrold *et al.*, 2017). While dispersal of adapted genotypes to a favorable new location may happen naturally by chance, management of key species could help facilitate this process in a controlled manner via assisted evolution or migration (Hoegh-Guldberg *et al.*, 2008, van Oppen *et al.*, 2017, van Oppen *et al.*, 2015). As a conservation strategy, assisted migration has been debated due to difficulties in predicting unintended consequences of introducing species to new habitats outside of their natural range (Ricciardi & Simberloff, 2009). In the ocean, however, there is a high chance of finding *spatial refugia* within the existing biogeographic range of a species due to the vast spatio-temporal heterogeneity of seawater CO_2 chemistry within ocean microclimates (Chan *et al.*, 2017, Kapsenberg & Hofmann, 2016, Vargas *et al.*, 2017). Assisted migration across OAR combines management actions addressing both adaptive capacity and exposure, and may be particularly beneficial to sensitive species with a large biogeographic range but small dispersal distance.

Management guidelines

Management guidelines for land-based climate change refugia can readily be applied to the marine realm. A step-by-step workflow, developed by Morelli *et al.* (2016) and adapted for OAR is as follows: (1) Identify clear management goals, which includes pinpointing the organism and biological process of interest for conservation. (2) Assess vulnerability of the target resource as a function of sensitivity, exposure, and adaptive capacity. This will require knowledge and integration of environmental variability in biological experiments either by using the existing literature or designing new studies, which will be ambitious beyond the scope of an individual species or marine resource. (3) Revise management goals based on the vulnerability assessment in Step 2. (4) Identify locations of potential refugia based on historical, environmental, modeling, and biological data. Evaluate if these conditions support the management goals and are likely to persist through the expected duration of anthropogenic ocean acidification or need of the target marine resource. (5) Prioritize refugia for management by evaluating other benefits of its location, such as overlap with other vulnerable resources, existing marine protected areas, and site accessibility. (6) Identify and implement management actions. (7) Monitor refugia and adjust management actions to maintain management goals.

For OAR, *spatial* and *adaptive refugia* have the potential to target multiple species at once. From a practical perspective, priority locations for OAR research could therefore be chosen based on existing marine protected areas that exhibit the right environmental characteristics. Inter- and intra-specific vulnerability assessments will be necessary to assess management goals. For example, the environmental conditions that shape *adaptive refugia* for sea urchins can be harmful to the early development and aquaculture production of oysters (Barton *et al.*, 2012). *Small-scale operative refugia* will most likely benefit a target marine resource or species. As some biological responses showed negative responses to CO_2 variability regimes (14%), inclusion of CO_2 variability remains an important aspect of vulnerability assessments, especially for refugia targeting a single species. Temporal variability in seawater CO_2 chemistry can differentially affect biological processes even within the same life history stage (Kapsenberg *et al.*, 2018), and an understanding of vulnerability through life stages may also be necessary. Organisms are likely to encounter a range of stressors within their environments, and CO_2 chemistry may not be the predominant one. For example, mortality in shellfish aquaculture is driven by ocean acidification in the Northeast Pacific upwelling system (Barton *et al.*, 2015), summer heat stress in the Ebro Delta on the Spanish Mediterranean coast (M. Fernández pers. comm.), and salinity stress associated with extreme events (Cheng *et al.*, 2016). Therefore, if a refugium is targeting ocean acidification impacts, it is important to determine that changes in CO_2 chemistry represent a primary stressor. Once an OAR has been identified, several ocean management actions can be implemented to improve overall ecosystem health (Gattuso *et al.*, 2018), regardless if one is managing for exposure or adaptive capacity. Effective OAR management will require a holistic view of ecosystems, encompassing the diverse array of processes that alter CO_2 chemistry (Fig. 1, Box 1) and may often require the coordination of several management actions operating across disciplines.

Considerations for future research

As research will play a large role in identifying OAR, we briefly highlight two general knowledge gaps in ocean acidification biology. First, identifying OAR in a specific area requires knowing to which aspect of CO_2 chemistry (*e.g.,* pH, pCO_2, Ω) the target organism and biological process are sensitive and how those parameters are expected to change over time. The latter can be achieved with high spatio-temporal resolution of oceanographic measurements and modeling (Chan *et al.*, 2017, Cyronak *et al.*, 2018, Koweek *et al.*, 2018, Krause-Jensen *et al.*, 2015). However, for most all biological processes, the mechanism and reaction norm (*i.e.,* sensitivity measured across a wide range of exposures) by which a specific parameter of CO_2 chemistry affects an organism remains unclear (Bach, 2015, Cyronak *et al.*, 2016, Hendriks *et al.*, 2015). Different CO_2 parameters can differentially influence various biological processes, even within a single species (Waldbusser *et al.*, 2015). Identifying mechanisms of biological sensitivity to changes in CO_2 chemistry is especially important for coastal areas where various CO_2 parameters can decouple due to changes in temperature and salinity driven by watershed inputs (Box 1) (Fassbender *et al.*, 2016, Waldbusser & Salisbury, 2014).

Second, once the driver of ocean acidification sensitivity is known for a given species it will be easier to design and interpret experiments assessing impacts of multiple stressors (Boyd *et al.*, 2018). This research should be conducted in a way that complements the environmental variability that is observed in an organism's environment. Parameters such as salinity, oxygen, and temperature can exhibit large natural spatial and temporal variability, and multiple stressors do not necessarily occur synchronously in time (Gunderson *et al.*, 2016). For example, seasonal changes in diel processes can result in asynchronous warming and acidification stress on coral reefs (Kline *et al.*, 2015). Exposure to multiple stressors is not always a simple scenario of warming and acidification, and local variability regimes may be more important than changes in global means (Boch *et al.*, 2018, Boyd *et al.*, 2018, Reum *et al.*, 2016). For instance, some studies show negative effects of pH variability only when low pH coincides with instances of hypoxia (Gobler *et al.*, 2017, Lifavi *et al.*, 2017). Successful research in the area of OAR will require multidisciplinary approaches that aim to not only determine functional relationships, but create mechanistic understandings of how biological processes respond to local environmental conditions in the context of ocean acidification.

Conclusions

In the marine realm, dynamic CO_2 variability in marine ecosystems provides the opportunity for local ocean acidification management by taking advantage of natural heterogeneity in species vulnerability. Specifically, OAR based on seawater CO_2 chemistry can either; (1) reduce exposure to harmful conditions via sustained elevated mean pH, or, (2) boost adaptive capacity via frequent exposure to low and variable pH. While rapid and sweeping international reduction of CO_2 emissions should remain the primary goal, local management of ocean acidification may be necessary to ensure the persistence of marine ecosystem services and resources. With this in mind we outline some of the most important considerations moving forward:

- When assessing the effectiveness of OAR, environmental conditions must be connected to a biological benefit such that a species overall vulnerability to ocean acidification is reduced.
- OAR based on exposure, whether natural (*spatial refugia*) or purposeful (*small-scale operative refugia*), must exhibit a significant and sustained increase in mean pH compared to surrounding waters, regardless of temporal variability regimes.
- OAR that boost adaptive capacity (*adaptive refugia*) are most likely to be found at areas with frequent low pH events and intense CO_2 variability (*i.e.,* exposure hotspots). As of now, the potential of *adaptive refugia* is largely based on evidence from non-photosynthesizing calcifiers from temperate marine ecosystems.
- Conservation of an OAR is only relevant if the characteristics of the refugia persist through time, such that the target species can endure for the duration of anthropogenic ocean acidification or necessity of the marine resource (*e.g.,* aquaculture). This is particularly important in the assessment of OAR based on primary production as a means to mitigate ocean acidification exposures.
- Marine protected areas will likely support the effectiveness of any OAR by reducing other local stressors (*e.g.,* pollution, habitat destruction) and maximizing genetic diversity and healthy, large populations (Roberts *et al.*, 2017).
- Future research on the mechanistic understanding of ocean acidification sensitivity and variability in multi-stressor exposures will advance the assessment and implementation of OAR. This may require consideration of an organism's full life history.

This perspective is not meant to provide a definitive list of local ocean acidification management options. Rather, the ideas outlined here are intended to apply the current research to management actions. There will be a finite source of time, funding, and effort to implement any local management action, and it is important to develop clear goals and assess the potential return on investment. For example, while phytoremediation may seem like a 'no regrets' investment due to other ecological benefits (Nielsen *et al.*, 2018), resources that go into these efforts with the intention of combatting ocean acidification may fall short of desired objectives. Research on OAR remains a hot topic, but an effective way forward requires the synthesis of multidisciplinary research that integrates interdisciplinary perspectives from the organism to the ecosystem, alongside targeted and goal-oriented management planning. Ultimately, the local management of global change represents an immensely challenging endeavor, and successful enterprises will require synergy between interdisciplinary science and feasible management actions.

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Box 1. Seawater CO_2 chemistry dynamics in marine ecosystems

An organism's exposure to seawater CO_2 chemistry is driven by a hierarchy of biogeochemical and physical processes extending from the open ocean to the organism's boundary layer (Fig 1). The magnitude of contemporary variability in CO_2 chemistry is often greater than the end-century predictions for ocean acidification, which can either amplify or alleviate the harmful exposures associated with anthropogenic ocean acidification (Hofmann *et al.*, 2011). Increasing seawater CO_2 concentrations shift chemical equilibria to induce a suite of changes in biologically important parameters such as pH, $p\mathrm{CO}_2$, saturation state (Ω), and bicarbonate concentrations ($[\mathrm{HCO}_3^-]$), among others (Waldbusser & Salisbury, 2014, Zeebe & Wolf-Gladrow, 2001). Depending on the driver, CO_2 parameters can decouple, complicating estimates of ocean acidification impacts in some ecosystems. For the purposes of this paper, we collectively refer to spatio-temporal variability in one or all of these parameters as variations in seawater 'CO_2 chemistry.'

Seawater CO_2 chemistry is modified seasonally and latitudinally due to differences in solar irradiance and temperature, which can influence the duration of primary production (Racault *et al.*, 2012, Takahashi *et al.*, 2002). For example, seasonal decoupling of pH and aragonite saturation state (Ω_{ar}) occurs in the Mediterranean Sea and North Atlantic due to summertime warming (Courtney *et al.*, 2017, Kapsenberg *et al.*, 2017a). In contrast, summertime primary production in the Southern Ocean causes significant increases in both pH and Ω_{ar} during seasonal phytoplankton blooms (Kapsenberg *et al.*, 2015, McNeil *et al.*, 2011).

Regional event-scale processes (few days to a few months) such as phytoplankton blooms (Kapsenberg & Hofmann, 2016), upwelling (Chan *et al.*, 2017), and freshwater contributions from precipitation, runoff, and groundwater (Fassbender *et al.*, 2016) further modify CO_2 exposures. Upwelling off of the California coast frequently results in pH exposures below pH 7.8 (Chan *et al.*, 2017, Feely *et al.*, 2008), while phytoplankton blooms and overall community production can increase pH by 0.1 – 0.2 units (Frieder *et al.*, 2012, Kapsenberg & Hofmann, 2016). Freshwater sources themselves vary drastically in carbonate chemistry, thereby disparately influencing CO_2 chemistry dynamics across salinity gradients (Fassbender *et al.*, 2016). For example, freshwater total alkalinity can be either lower or higher than seawater, which can change how watershed inputs impact the surface water CO_2 chemistry of nearshore ecosystems (Cyronak *et al.*, 2014a, Millero *et al.*, 2001).

At the habitat scale (1 m – 1 km), benthic community metabolism drives diel pH variability via shifts in photosynthesis and respiration (Hendriks *et al.*, 2014, Kapsenberg & Hofmann, 2016). Seabed composition (*e.g.,* calcium carbonate and silicate sediments, hard bottom, etc.) and local hydrology (*e.g.,* tides, currents, residence times, and groundwater) can also influence CO_2 chemistry at these scales (Burdige *et al.*, 2010, Santos *et al.*, 2011, Zhang *et al.*, 2012). At the smallest spatial scale (mm's to cm's), seawater may be modified within an organism's diffusive boundary layer due to the metabolism of the organism itself (and the host organism for epibionts) along with physical properties that determine the size of the boundary layer, such as benthic structure and flow rates (Hurd *et al.*, 2011, Noisette & Hurd, 2018).

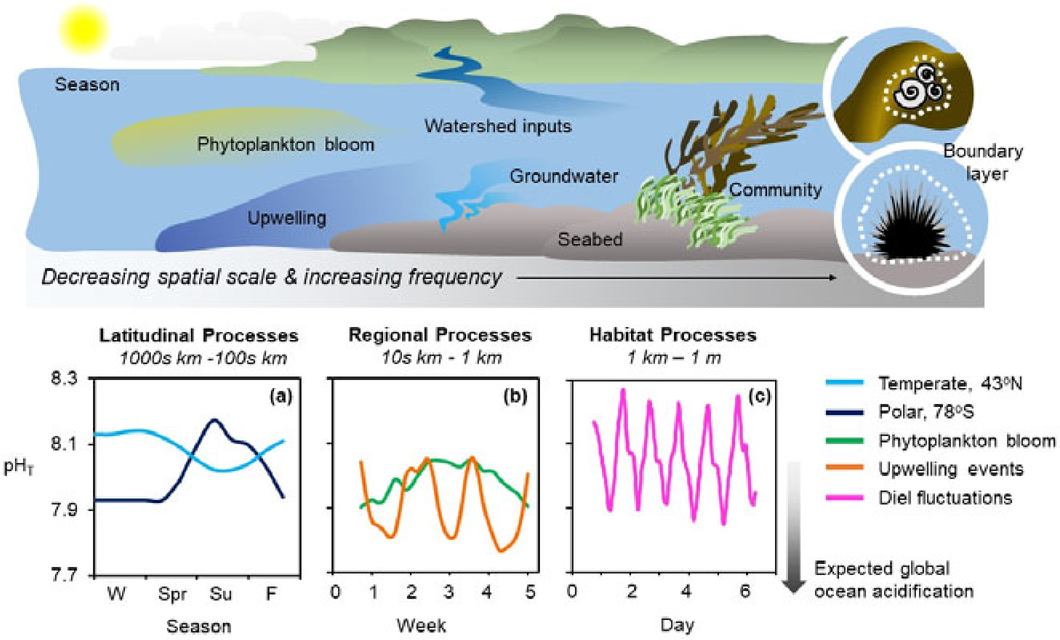
Drivers of CO_2 chemistry can interact over frequencies, such that multiple drivers can act together at any given location. The importance of each driver of seawater CO_2 chemistry, in terms of exposure, may change through time. For instance, the magnitude of diel variability can vary seasonally (Kapsenberg & Hofmann, 2016, Murray *et al.*, 2014) and an upwelling event could have overwhelmingly harmful effects on organisms (Barton *et al.*, 2012, Bednaršek *et al.*, 2012). Taken together, the dynamic nature of CO_2 chemistry in marine ecosystems creates unique palettes of exposure in time and space.

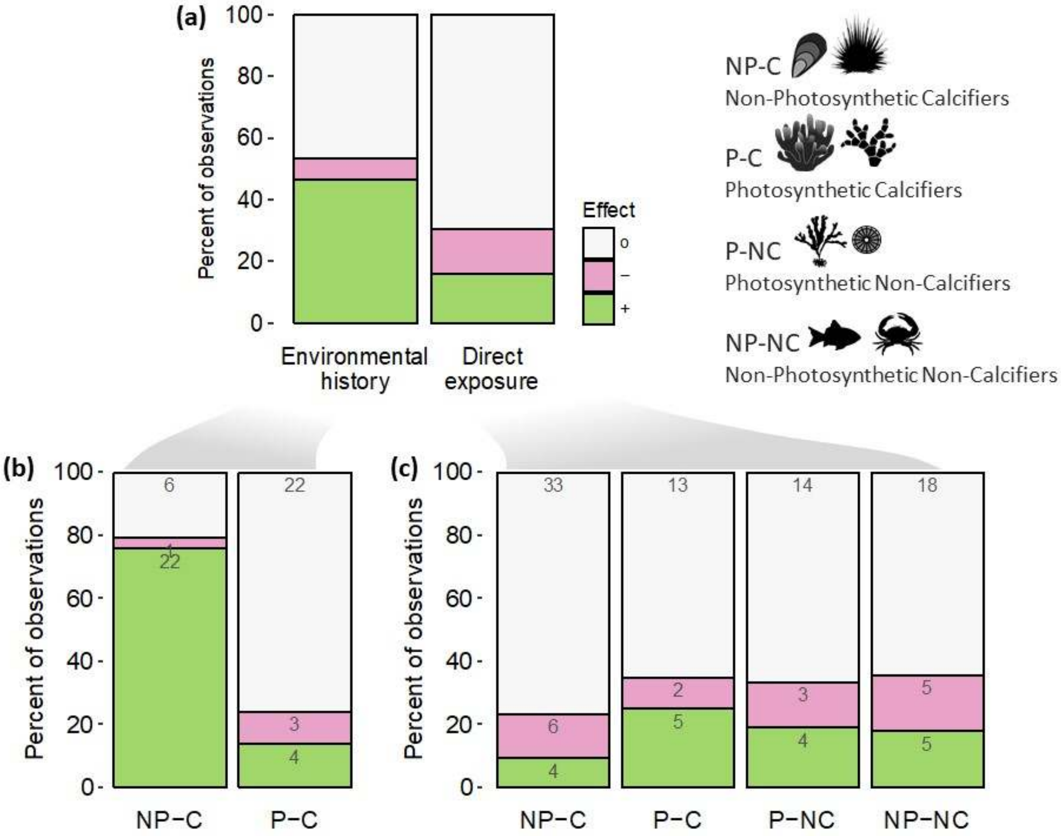
Box 2. Ocean acidification refugia definitions and potential examples

<table>
<tr><td colspan="3">Ocean Acidification Refugia - <i>Any area of the coastal or open ocean that exhibits persistent environmental conditions such that a species' vulnerability to anthropogenic ocean acidification is reduced, where vulnerability is the combination of sensitivity, exposure, and adaptive capacity</i></td></tr>
<tr><th colspan="2">EXPOSURE</th><th>ADAPTIVE CAPACITY</th></tr>
<tr><th>Spatial refugium</th><th>Small-scale operative refugium</th><th>Adaptive refugium</th></tr>
<tr><td><i>An area within a species biogeographic range that experiences less intense ocean acidification exposure relative to sister populations</i></td><td><i>An area that experiences less intense ocean acidification exposure due to purposeful CO_2 management</i></td><td><i>An area that enhances a species' adaptive capacity to ocean acidification, often an exposure hotspot</i></td></tr>
<tr><td>▪ Upwelling-shielded microclimates
▪ Shallow deep-sea mounts
▪ Primary production hotspots (!)</td><td>▪ Phytoremediation (!)
▪ Bubble stripping (!)
▪ Alkalization</td><td>▪ Upwelling zones
▪ Estuaries
▪ Tidepools</td></tr>
<tr><td colspan="3">(!) Refugia dependent on primary producers</td></tr>
</table>

Figure 1. Processes modifying ocean acidification exposures over a range of temporal frequencies and spatial scales. (a) Seasonal pH regimes driven by warming in a temperate ecosystem and primary production in a polar ecosystem (Kapsenberg *et al.*, 2017a, Kapsenberg *et al.*, 2015). **(b)** Event-scale pH variability over a period of 5 weeks. Primary production by a phytoplankton bloom increases pH which decreases upon succession of the bloom, while periodic upwelling events cause strong decreases in pH (Kapsenberg, 2015, Kapsenberg & Hofmann, 2016). **(c)** Intense diel pH fluctuations in a coral reef ecosystem driven by benthic photosynthesis and respiration (Cyronak *et al.*, 2014a). *See Box 1 for more details.*

Figure 2. Biological responses to CO_2 variability in the context of ocean acidification. (a) Responses grouped by experimental design. **(b)** Responses from environmental history studies only, grouped by mode of life (not shown: one positive observation each for P-NC and NP-NC). **(c)** Responses from direct exposure studies, grouped by mode of life. Responses are either positive (green, variability mitigates ocean acidification effect), negative (pink, variability exacerbates ocean acidification effect), or neutral (white, variability has no effect). Numbers within bars denote the number of observations.


Season
Phytoplankton bloom
Watershed inputs
Groundwater
Upwelling
Community
Seabed
Boundary layer
Decreasing spatial scale & increasing frequency
Latitudinal Processes
1000s km -100s km
Regional Processes
10s km - 1 km
Habitat Processes
1 km – 1 m
8.3
8.1
7.9
7.7
pH_T
(a)
(b)
(c)
W
Spr
Su
F
Season
0
1
2
3
4
5
Week
0
2
4
6
Day
Temperate, 43°N
Polar, 78°S
Phytoplankton bloom
Upwelling events
Diel fluctuations
Expected global ocean acidification


(a)
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Percent of observations
Environmental history
Direct exposure
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NP-C
Non-Photosynthetic Calcifiers
P-C
Photosynthetic Calcifiers
P-NC
Photosynthetic Non-Calcifiers
NP-NC
Non-Photosynthetic Non-Calcifiers
(b)
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80
60
40
20
0
Percent of observations
6
1
22
22
3
4
NP–C
P–C
(c)
100
80
60
40
20
0
Percent of observations
33
6
4
13
2
5
14
3
4
18
5
5
NP–C
P–C
P–NC
NP–NC