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Review

Ocean acidification: Linking science to management solutions using the Great Barrier Reef as a case study

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ABSTRACT

Coral reefs are one of the most vulnerable ecosystems to ocean acidification. While our understanding of the potential impacts of ocean acidification on coral reef ecosystems is growing, gaps remain that limit our ability to translate scientific knowledge into management action. To guide solution-based research, we review the current knowledge of ocean acidification impacts on coral reefs alongside management needs and priorities. We use the world's largest continuous reef system, Australia's Great Barrier Reef (GBR), as a case study. We integrate scientific knowledge gained from a variety of approaches (e.g., laboratory studies, field observations, and ecosystem modelling) and scales (e.g., cell, organism, ecosystem) that underpin a systems-level understanding of how ocean acidification is likely to impact the GBR and associated goods and services. We then discuss local and regional management options that may be effective to help mitigate the effects of ocean acidification on the GBR, with likely application to other coral reef systems. We develop a research framework for linking solution-based ocean acidification research to practical management options. The framework assists in identifying effective and cost-efficient options for supporting ecosystem resilience. The framework enables on-the-ground OA management to be the focus, while not losing sight of CO_2 mitigation as the ultimate solution.

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1. Introduction

Approximately 30% of the carbon dioxide (CO_2) produced by human activities has been absorbed by the world's oceans (IPCC AR5 WG1, 2013). On entry into the ocean, CO_2 reacts with seawater causing a decrease in pH and the concentration of dissolved carbonate ions, [CO_3^{2-}], a process referred to as 'ocean acidification' (OA). Since preindustrial times, the pH of surface ocean waters has decreased by approximately 0.1 pH units, which equates to an increase in "acidity" (i.e., hydrogen ion concentration) of approximately 30%. Over the same timeframe, carbonate ion concentrations in surface waters have decreased by 11% in the tropical oceans and 15% in the Southern Ocean (Orr et al., 2005). Current levels of surface water pH are now outside those seen over the past million years and could exceed those of the last 40 million years sometime this century (Pelejero et al., 2010).

Major changes in ocean chemistry can have profound effects on marine ecosystems (Doney, 2010) and have even been implicated in creating conditions leading to past mass extinction events (Clarkson et al., 2015; Veron, 2008). Coral reefs are one of the world's most vulnerable marine ecosystems to OA with a wide range of impacts expected for corals, fish, marine algae and many other reef organisms (Andersson et al., 2011; Hoegh-Guldberg et al., 2007; Przeslawski et al., 2008). These impacts range from reduced calcification and increased rates of erosion and dissolution of calcareous structures to changes in respiration, photosynthesis, gas exchange, and recruitment (Andersson et al., 2011; Dove et al., 2013). Coral communities around natural CO_2 seeps show shifts in community composition from highly diverse and structurally complex communities to those characterized by much lower diversity and structural complexity (Fabricius et al., 2011), leading to loss of ecological function and associated ecosystem services.

Despite the growing concern for the impacts of ocean warming and acidification on coral reef ecosystems, the primary recommendation to management and regulatory bodies has been to mitigate local stressors such as land-based sources of pollution and overfishing because climate change and OA have limited management levers at the local level (Falkenberg et al., 2013; Hughes et al., 2010; Kennedy et al., 2013; Maina et al., 2011; McClanahan et al., 2014; Mcleod et al., 2012, Pandolfi et al., 2011). The rationale is often that intensified management of local pressures supports reef resilience by reducing exposure to multiple stressors, thereby improving the likelihood of minimising negative impacts of ocean acidification and warming. Such local resilience-based management only works up to a point, beyond which the impacts of ocean acidification and warming will overwhelm local management benefits (Anthony et al., 2015). The perceived infeasibility of managing for OA is exacerbated by a lack of scientific studies designed to address conservation planning and management priorities (Mcleod et al., 2012).

Here, we assess how OA research can be best advanced to support management needs and priorities for the world's largest continuous reef system, the Great Barrier Reef (GBR, Fig. 1). Stretching over 2100 km, the Great Barrier Reef Marine Park (GBRMP) and the adjacent Coral Sea Commonwealth Marine Reserve are among the world's largest coral reef regions under management. This vast region generates approximately $AUD 6 billion in direct revenue each year from tourism and fishing (GBRMPA, 2013). In addition to these tangible benefits, the GBR forms a critical part of Australia's natural heritage; it is recognized as one of Australia's most visible icons and in 1981 was given World Heritage status by the United Nations Educational, Scientific, and Cultural Organization (UNESCO). Notably, the GBRMP Authority has been managing the GBR in partnership with the Queensland Government and other agencies since 1975, serving as a durable example of coral reef management that has broad applications for coral reefs worldwide.

Despite the legacy of management in the GBRMP, the health of the GBR is in a state of decline, with an estimated 50% loss in coral cover between 1985 and 2012 (De'ath et al., 2012). In 2015–2016, the GBR suffered the worst mass bleaching event on record, in which 93% of the 911 surveyed reefs experienced bleaching. It is critically important to bolster the resilience of the GBR, and to maximise its natural capacity to recover. There is considerable experimental evidence indicating that OA compromises the ability of coral communities to recover from disturbances by slowing recruitment, growth and calcification (Andersson et al., 2011). In this way, OA, combined with factors such as overfishing and pollution, serves to reduce the resilience of coral reefs, shifting the balance away from net growth towards net loss. Improvements in management are critical to attempt to secure the long-term health of the GBR (Hughes et al., 2015), and understanding the responses of reefs to both global and local stressors is critical for management plans to be effective (Anthony et al., 2015). The key objectives of this paper are to: 1) characterise OA as a stressor on coral reefs and how it is likely to impact ecosystem goods and services; 2) identify management priorities and potential strategies to help address acidification-related threats; 3) identify knowledge gaps that limit effective management responses now and in the future; and 4) outline a strategy that integrates research and development with management planning to deliver effective solutions to the OA problem on the GBR.

2. Ocean acidification on the Great Barrier Reef

A brief review of the effects of OA on the GBR frames our discussion of the scientific needs of management. The goal of this paper is not to review the effects of OA on all reef-associated processes, but to identify existing knowledge gaps that limit management responses. To this end, the following is a brief overview of the strengths and weaknesses in our present understanding of the impacts of OA on the GBR in three key areas: 1) chemical changes; 2) impacts on reef organisms; and 3) perturbations to coral reef ecosystems.

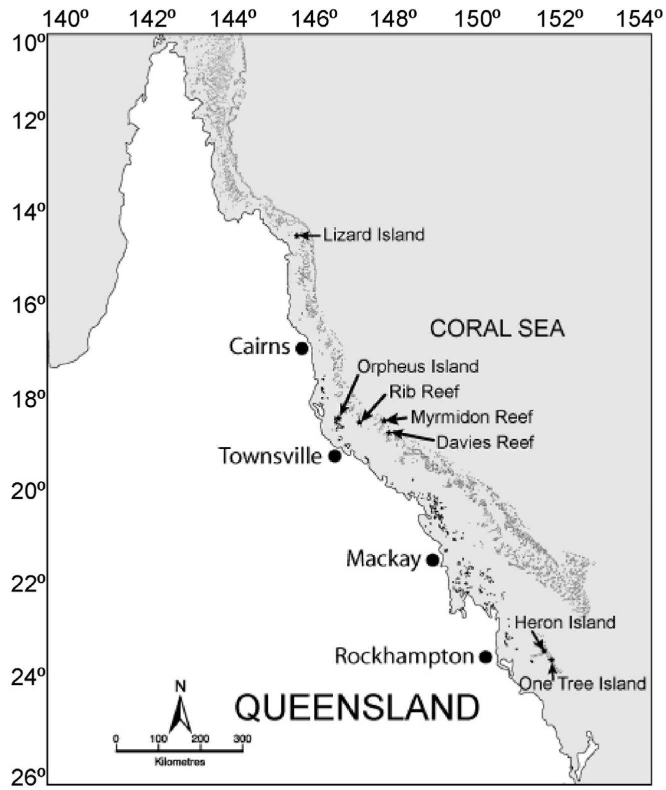

Fig. 1. Map of the Great Barrier Reef off the coast of Queensland, Australia (www.imos.org.au).

2.1. Chemical changes

Understanding the natural spatial (within-reef, cross-shelf, latitudinal) and temporal (diel, seasonal, past historic and projected future) variability of the seawater carbonate system is critical to assess the sensitivity of reef communities to future changes in ocean chemistry (Hofmann et al., 2011; Mcleod et al., 2012). We still have limited understanding of the spatial and temporal patterns in seawater carbonate chemistry on the GBR and surrounding waters–and of the main drivers of change. Preliminary work indicates a high degree of variability in carbonate chemistry driven by a combination of physical forcing such as temperature, biological carbon exchanges between the water column and benthic fauna and flora (Albright et al., 2013; Anthony et al., 2013; Kleypas et al., 2011; Kline et al., 2012), and large-scale mixing between GBR shelf water and the Coral Sea (Uthicke et al., 2014). A key question for managers is whether reef communities in variable environments are highly adapted/acclimated to fluctuating conditions and thus future changes in ocean chemistry, or whether they are residing near the limit of their tolerance levels and, are thus, highly vulnerable to projected OA. Despite an increasing number of studies documenting the inherent diel and seasonal variability of parts of individual reefs (Albright et al., 2013, 2015; Falter et al., 2013; Gagliano et al., 2010; Shaw et al., 2012; Silverman et al., 2012, 2014), there is a limited amount of work on whole-of-reef and whole-of-GBR scales (Shaw and Mcneil, 2014; Suzuki et al., 2001; Uthicke et al., 2014); consequently, our understanding of feedbacks in the system is underdeveloped. Establishing carbonate chemistry baselines and generating coupled hydrodynamic-chemical-biological models of the GBR (e.g (Mongin and Baird, 2014; Schiller et al., 2014)., would: 1) inform the understanding of changes in carbon chemistry through time; and 2) help identify areas of the GBR that are most vulnerable to OA.

2.2. Organism-level responses

2.2.1. Reef builders – eroders

OA impairs early life stages such as, fertilization, growth and survivorship of new recruits, and skeletal growth in many coral and coralline algal species, with species common to the GBR showing similar responses to those reported elsewhere (Anthony et al., 2008; Diaz-Pulido et al., 2012). At CO_2 seeps in Papua New Guinea–which is part of the same biogeographic region as the GBR–the diversity of coral species (Fabricius et al., 2011) and the percent cover of coralline algae (Fabricius et al., 2015) decline steeply along CO_2 gradients, resulting in shifts in community structure from highly diverse and structurally complex communities (e.g., *Acropora* dominated) to communities characterized by much lower diversity and structural complexity (e.g., *Porites* dominated). Reduced structural complexity undermines the ecological function and ecosystem services of coral reefs by compromising their ability to provide habitats for a variety of fish and invertebrate species (Jones et al., 2004). In addition to direct impacts on reef builders, OA and warming have been shown to accelerate decalcification of GBR coral communities, with microbial communities (Dove et al., 2013), endolithic algae (Reyes-Nivia et al., 2013) and excavating sponges (Fang et al., 2013) being the primary agents of erosion. Because reef growth depends on the positive balance between constructive (calcification, cementation) and destructive (dissolution, erosion) processes, it is critical to better understand the projected impacts of OA on the carbonate budget (Perry et al., 2012).

2.2.2. Fish and fisheries

While growth and survival of adult marine fish are generally considered to be tolerant to moderate increases in CO_2 (Melzner et al., 2009), changes in the concentrations of acid-base relevant ions disrupt neuroreceptor function in several GBR fish species, resulting in profound changes in behaviour and sensory responses (Chivers et al., 2014; Nilsson et al., 2012); these impacts can have cumulative effects on the timing of settlement, habitat selection, and survivorship (Munday et al., 2010, 2012a). Exposure of parents to high CO_2 may ameliorate the negative effects of high CO_2 on juvenile growth and development of some GBR fish species (Miller et al., 2012); however, parental exposure does not appear to mitigate the effects of OA on the sensory biology and behaviour of larval and juvenile fishes (Welch et al., 2014).

Acidification-induced effects on larval and juvenile fish behaviour have the potential to dramatically alter population dynamics of key species (Munday et al., 2010), some of which may have important fisheries value. Studies of ecologically and economically significant reef species are few; however, one recent study reported sensory and behavioural impairment (including attraction to predator scent) in juvenile coral trout at near-future pCO_2 levels (Munday et al., 2012b). Coral trout is a major target species for commercial reef-based fisheries in Australia and is estimated to account for >50% of the total commercial catch for the Coral Reef Finfish Fishery (CRFFF) on the GBR (Mapstone et al., 1996). Unfortunately, our understanding of the impacts of OA on GBR fisheries – as elsewhere – is limited; however, studies of United States-based fisheries indicate that impacts including decreased revenue (potentially tens of billions of dollars), job losses, and indirect economic costs may occur if OA broadly damages marine habitats, alters marine resource availability, and disrupts other ecosystem services (Cooley and Doney, 2009).

2.3. Ecosystem-level responses

Laboratory experiments show that OA has the potential to affect the physiology, development, growth and behaviour of key reef organisms. It is, however, extremely difficult to extend species-level effects to wider ecosystem consequences (Gaylord et al., 2015). Because sensitivity to OA varies among taxa and their life stages, increasing CO_2 has the potential to alter biodiversity, trophic and competitive interactions, recruitment dynamics and other ecosystem functions (Fabricius et al., 2014; Russell et al., 2012). The scope for acclimatization and adaptation will further influence ecosystem-scale outcomes (Sunday et al., 2014). Available study systems for investigating community and ecosystem-scale responses of coral reefs to OA include: multi-species, long-term mesocosms (Dove et al., 2013); flumes, conducted either in-situ (Kline et al., 2012) or in the laboratory (Anthony et al., 2011a); volcanic, shallow-water CO_2 seeps (Fabricius et al., 2011; Munday et al., 2014); and areas with naturally high CO_2 variability such as reef lagoons or embayments; (Duarte et al., 2013; Price et al., 2012). Results from these study systems suggest that OA will cause profound, ecosystem-wide changes in coral reefs, including: decline of calcifying taxa such as coralline algae (Fabricius et al., 2011); loss of three dimensional structure as coral communities shift from structurally complex species to massive species (Fabricius et al., 2011); altered settlement substrata, including loss of coralline algae, resulting in reduced coral recruitment (Fabricius et al., 2011, 2015); increased rates of bioerosion (Dove et al., 2013; Fang et al., 2013; Reyes-Nivia et al., 2013); increased abundance of macroalgae and seagrasses (Fabricius et al., 2011); and altered sediment properties (Eyre et al., 2014). At CO_2 seeps in Papua New Guinea, reef development ceases at mean pH values below 7.8, suggesting that this value acts as a terminal threshold for coral reef development in this location (Fabricius et al., 2011). Given the complexities of ecosystem-scale responses to OA, it is important to not only take advantage of existing study systems (mesocosms, CO_2 seeps, etc.) but to continue developing new strategies for assessing ecosystem-scale effects of OA; the development of integrated modelling and observational studies will be critical (discussed further below).

3. Management

3.1. Current management of GBR

The Great Barrier Reef is a joint Queensland and Federal Marine Park and a World Heritage Area. The GBRMP has been managed as a multiple use marine park jointly by the different levels of government since it was established through the GBRMP Act in 1975. The jurisdictional arrangements include the Great Barrier Reef Marine Park Authority (GBRMPA, a statutory independent Authority), Queensland, and the Department of Environment. Reef management is governed by the GBRMP Act plus the Reef 2050 plan, which is the overarching framework for protecting and managing the Great Barrier Reef from 2015 to 2050; the 2050 plan is a key component of the Australian Government's response to the recommendations of the UNESCO World Heritage Committee. Every five years, the GBRMPA publishes an Outlook Report that evaluates the reef's health, pressures, and management effectiveness; these reports are required under the GBRMP Act 1975 and aim to provide a regular and reliable means of assessing reef health and management. The 2014 report found that the greatest risks to the Reef are climate change, land-based run-off, and coastal development, with some remaining impacts of fishing (GBRMPA, 2014).

3.2. Management options

The only comprehensive solution to OA and global warming is to rapidly decrease anthropogenic emissions of CO_2 and other greenhouse gases to the atmosphere (i.e., mitigation). Nonetheless, given the legacy of existing fossil fuel-based infrastructure and the rapidly growing global demand for energy, continued ocean acidification is expected even under the most optimistic emissions scenarios (IPCC AR5 WG1, 2013). Also, it will take thousands of years to remove the anthropogenic CO_2 from the atmosphere and the surface oceans, by subduction into the deep oceans and neutralisation by sediment and rock dissolution (IPCC AR5 WG1, 2013). Given committed ocean acidification and warming, there is a growing need to develop regional and local management strategies to minimise ecosystem damage caused by the continued release of CO_2. The following is a discussion of such options that may be effective in the context of OA, partnered with a brief evaluation of their anticipated feasibility and efficacy. These considerations aim to guide the investment in and prioritisation of research to address what we identify to be the most viable management options for the GBR in the context of OA.

The underlying principles for managing the GBR for OA, and global change in general, are to (1) support resilience (i.e., enhance the health of the GBR so that it is better able to cope with stress); and (2) support adaptation (i.e., create conditions under which reef ecosystems will thrive in a changed ocean). The management and policy options available to achieve these goals, range from conventional strategies such as expanding marine protected areas and reducing secondary sources of stress like fishing pressure and contaminants in terrestrial runoff to unconventional options such as geochemical modification of seawater and ocean fertilization. These strategies can be applied in preventative (resisting change) and/or responsive (abating or recovering from change) ways (Gattuso et al., 2015).

At least four conventional strategies are used to support resilience and adaptation on coral reefs. Firstly, spatial risk spreading, or protecting replicates of major habitat types and bioregions and enforcing such protection, have proved successful on the GBR (Fernandes et al., 2005). Secondly, maximizing ecological connectivity within networks of ‘source’ and ‘sink’ reefs (e.g., removing anthropogenic barriers to adaptive capacity such as artificial barriers to dispersal) can help preserve genetic diversity, the raw material for evolutionary adaptation (Jones et al., 2009; Van Oppen and Gates, 2006). Thirdly, vigilant management of local- and regional-scale stressors, for example improved land-use management to reduce the pollution that contributes to lowered pH in coastal waters, are potentially effective means of supporting ecosystem resilience (Fabricius, 2011). Finally, management of fish stocks, in particular herbivores, are critical in helping prevent community shifts under combinations of warming, acidification and nutrient enrichment (Anthony et al., 2011b) because it seems likely that faster-growing algae may outcompete slower-growing corals under elevated pCO_2 (Diaz-Pulido et al., 2011; Mcleod, 2008; Mcleod et al., 2012).

In addition to conventional approaches, the demand for exploring unconventional options to help abate OA is likely to increase. Most of these options aim to restore ocean chemistry to its ‘normal’ state. Suggestions range from direct chemical intervention, such as adding scrubbing chemicals such as calcium hydroxide to stimulate CO_2 uptake (Rau et al., 2012), to the manipulation of community composition in order to facilitate photosynthetic uptake of CO_2 (Unsworth et al., 2012), Blue Carbon initiatives to manage carbon sequestration in coastal and offshore waters (Mcleod et al., 2011), and geoengineering solutions to tackle atmospheric CO_2 concentrations (Hardman-Mountford et al., 2013;

Vaughan and Lenton, 2011). The addition of artificial structures to offset habitat loss is also suggested (Rinkevich, 2005). Importantly, we must weigh the feasibility of each of these options in the context of global warming, potentially increasing intensity of tropical cyclones, extreme rainfall, and river flood events. Many of these approaches are unproven or impractical for areas as large as the GBR (~344,400 km^2), and further evaluation is needed to accurately assess which, if any, of these options are safe, cost-effective, and viable for mitigating OA impacts on coral reefs.

Given the uncertainty and lack of data surrounding a range of possible OA management actions, we focus here on two that have demonstrated benefits and reasonably low risks. To support resilience and adaptation of the GBR, we suggest that managers should prioritize actions addressing the following two objectives:

(1) Maintenance of large population sizes and genetic diversity.

To enhance evolutionary potential, one management option is to maintain large populations, where possible, thus maintaining genetic diversity on which natural selection can act over large spatial scales (Munday et al., 2013; Sunday et al., 2014). Maintaining the viability of different habitat-forming species such as branching coral species also provides resistance to stressors. For example, there is evidence from kelp forests that if the presence and health of habitat-forming species is maintained, the ability to resist ecological change is greatly enhanced (Falkenberg et al., 2012). Maintenance of large population sizes may be difficult given exposure to unmanageable stressors like storm damage from cyclones. Nonetheless, strategies for promoting large population size and genetic diversity include spatial planning (e.g., effectively managed marine protected areas) and managing secondary sources of stress including fishing pressure and water quality. An innovative method that may prove effective is assisted evolution in which well-adapted genotypes (Dixon et al., 2015) are targeted and promoted (Van Oppen et al., 2015). These methods, which involve selection but not genetic engineering, are well established in crop sciences (e.g (Varshney et al., 2005).), although forecasting which alleles will be most successful in a hypothetical future ocean is inherently uncertain.

(2) Understand and mitigate secondary/local sources of acidification by managing water quality.

Changing sediment loads from terrestrial sources and using controls on nutrient inputs as a policy lever for mitigating coastal water acidification can modify the carbonate chemistry of surface waters by altering the balance between autotrophy and heterotrophy (Bille et al., 2013). The GBR is located on a shallow continental shelf and receives run-off from 38 river catchments along its 2300 km long coastline, which drains 424,000 km^2 of coastal and inland Queensland (gbrmpa.gov.au). Inshore reefs, reefs that lie within 10 km of the coast, account for approximately 20% of the total number of GBR reefs and are under direct terrestrial influence from freshwater, sediment, nutrient, and organic carbon runoff (Uthicke et al., 2014). Preliminary work indicates that these reefs are subjected to elevated pCO_2 levels compared to offshore reefs and that the rate of increase in inshore pCO_2 is faster than offshore and atmospheric values (Cyronak et al., 2014; Uthicke et al., 2014). In the United States, local decision makers in several states including Alaska, Maine, Washington, California, and Oregon are starting to take action to mitigate local causes of acidification with existing legislation (Kelly et al., 2011; Strong et al., 2014). For the GBR, the ability of local representatives to make policy and management decisions that respond to, and in some cases, influence, the trajectory of coastal OA will be greatly enhanced by an improved understanding of the capacity of human activities and riverine dynamics to influence coastal carbonate chemistry.

Supporting ecosystem resilience and adaptation potential by maintaining large population sizes and mitigating secondary sources of acidification are tangible and effective strategies that are beneficial, regardless of OA (Bille et al., 2013). Nonetheless, management responses will need to be modified as the condition of the GBR changes, and options become fewer as warming and acidification worsen. Fig. 2 shows a theoretical framework for managing the GBR for OA in both space and time. The framework is grounded in risk theory, where managers employ lower-risk actions first such as conventional management options, and if/when those fail, move to increasingly higher-risk actions like unconventional management options (Rogers et al., 2015). For example, where and when the GBR is determined to be moderately affected by OA, the mitigation of local stressors and spatial planning to maintain large population sizes may be sufficient. As the relative threats from OA increase, either because the health and resilience of the GBR declines, its sensitivity increases, and/or the levels of exposure increase, unconventional management strategies may be deemed appropriate such as assisted migration, selective breeding, community manipulation, and/or chemical buffering. At any given time, managers are likely to need to work across Fig. 2 given the heterogeneity in the GBR. Some areas and values are already in very poor condition due to a range of impacts (Schaffelke et al., 2012; Thompson et al., 2012). It is also worth acknowledging the concept of lead-time; some research investment today is needed on longer-term questions in order to ensure solutions for tomorrow. The goal is to restore and enhance values, not just to protect and conserve; consequently, research identifying ways to bridge the gap between the actual and desired conditions of the GBR is essential.

4. Management-focused research

4.1. Research priorities

Our understanding of the effects of OA on chemical, organism-scale and ecosystem-scale processes is growing; however, gaps remain that limit our ability to translate scientific knowledge into management actions. We have summarized these knowledge gaps in the following eight key research priorities (Table 1):

1) What are the current chemical conditions on the GBR and how quickly are they changing?

Our understanding of the exposure of coral reefs to OA is directly related to our understanding of carbonate chemistry dynamics and rates of change. For evaluating management options and planning, improved understanding of the drivers of carbonate chemistry variability, as well as interactions and feedbacks in the system, is essential. Establishing baselines and developing carbonate chemistry 'maps' should be a priority. This can be achieved through sustained observations of carbonate chemistry at the individual reef and whole-of-region scales in conjunction with high spatial resolution models that simulate physical and biological feedbacks.

2) Which GBR regions are most and least sensitive to changes in seawater chemistry, and how does vulnerability vary in time and space?

Dynamic carbonate chemistry maps based on highly resolved spatial models (Priority 1), coupled with an understanding of the sensitivity of marine organisms and ecosystems (Priorities 3 and 6) are valuable management tools for identifying which geographic regions are most/least vulnerable to OA. While ambitious, initial

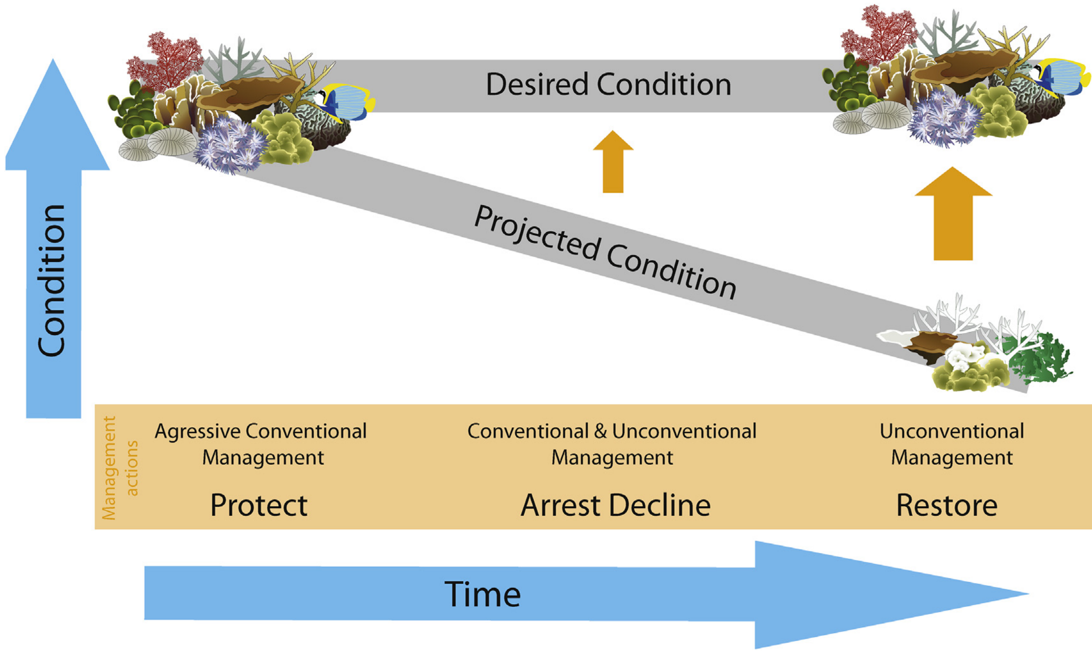

Fig. 2. Theoretical framework for managing the Great Barrier Reef (GBR) for ocean acidification in both space and time. The management focus adapts to changes in the condition of the reef through time (GBRMPA, 2014) while also proactively exploring new uncertain techniques of remediation. At any given time, managers likely need to work across Fig. 2 given the heterogeneity in the GBR. See text for details (Section 3.2 – 'Management Options').

steps could be centred on broad ecosystem types (e.g. sandy inter-reefal habitat, or coral-dominated communities) with the objective of increasing detail over time.

3) Which GBR species or groups are most and least sensitive to changes in seawater chemistry?

Knowledge of species-specific sensitivities will allow managers to prioritize species for protection. When used in conjunction with species distribution and carbonate chemistry maps, this knowledge will facilitate the production of 'vulnerability maps' to identify high and low risk regions. Studies on ecologically and economically significant reef species are also needed to interpret ecosystem-scale and socioeconomic consequences of OA (Priority 7). For example, two guilds that have not been well-studied are herbivores and bioeroders (e.g. parrot fishes, sea urchins), both groups that play a major role in the carbonate budget of reefs.

4) How does OA interact with other stressors (local and global) to influence organism and ecosystem responses?

There is growing evidence that local factors such as poor water quality and overfishing interact with global factors (Ekstrom et al., 2015; Maina et al., 2011). Our current understanding of these interactions is at an early stage but may be crucial for identifying potential impacts and solutions (Russell et al., 2009). For example, does OA enhance or reduce the thermal tolerance of reef organisms? How do OA and nutrients from terrestrial runoff alter the balance between autotrophy and heterotrophy in reef systems? How do OA, warming and increasing tropical cyclone intensity affect the structural integrity of reefs, and the balance between accretion and erosion? Can we limit synergies between stressors by managing local pollution (Falkenberg et al., 2013)? Providing answers to these questions, e.g., through the use of multi-stressor experiments, may directly influence management strategies (Przeslawski et al., 2015).

5) What is the ability of organisms to acclimatize and/or adapt to changing environmental conditions?

Although several studies indicate the potential for adaptation (Dixon et al., 2015; Palumbi et al., 2014), there is currently limited evidence that genetic adaptation in corals and other reef organisms will keep pace with some of the most rapid changes in ocean chemistry in geological time. What may be important in the immediate and short term is acclimatization, whereby phenotypic plasticity and epigenetic changes facilitate persistence, potentially buying time for genetic adaptation to catch up (Munday et al., 2013). Knowledge gaps call for answers to questions including: To what extent does parental exposure mitigate offspring response? Do populations contain sufficient adaptive genetic variation to favour rapid evolution to OA? Long-term and multigenerational studies (Van Oppen et al., 2015), quantitative breeding designs (Dixon et al., 2015; Foo et al., 2014; Munday et al., 2013; Sunday et al., 2014), and modern molecular approaches (Palumbi et al., 2014) are powerful tools to address these questions and may help managers identify solutions to support adaptation.

6) How will OA affect the overall ecosystem function of the GBR?

The effectiveness of management plans ultimately hinges on a more complete understanding of community and ecosystem-level responses. Studies are needed to resolve how OA will impact a range of species interactions, ecosystem processes and ecosystem responses including, but not limited to: food webs and trophic structures; habitat quality, including habitat structure, substratum composition, and benthic biofilms; the balance between reef accretion and erosion (i.e., the overall carbonate budget); weakened skeletal strength and implications for cyclone damage (Madin et al., 2012); settlement and recruitment dynamics, which influence rates of recovery post disturbance; productivity; grazing rates; competition; predator-prey relationships, and more. Where possible, laboratory experiments should be carried out in combination with

Table 1
Summary of OA research priorities to advance management goals (adapted from GBR Climate Change Adaptation Strategy and Action Plan). Asterisks refer to novel priorities that have not been emphasized in previous efforts (e.g., McLeod et al., 2012).

Research priorities	Science needed to support goal	Management focus area
1) Establishing carbonate chemistry maps (including current conditions and rates of change).	Continued development of mapping and monitoring efforts to produce carbonate chemistry maps of the reef Research targeting an improved understanding of drivers of variability and feedbacks in the system Hindcast and near real-time biogeochemical models to provide high spatial resolution maps of carbon chemistry parameters	Situation reporting and early warning tools
2) Identification of species and species groups that are most and least sensitive to OA.	Experiments to constrain organism/community response; where possible, create species vulnerability rankings Experiments targeting acclimatization and adaptation potential (e.g., parental effects, molecular mechanisms)	Prioritisation of species for protection Understanding socio-economic implications
3) Identification of geographic regions most and least sensitive to OA now and over time.*	Integrate carbonate maps, vulnerability rankings for taxa, species distribution maps, and local knowledge to create vulnerability maps for the reef Analysis of high resolution biogeochemical models	Prioritisation of areas for protection/spatial planning
4) Determine the interactive effects of OA with other global and local stressors on organism and ecosystem responses.	Multi-stressor experiments (laboratory and field-based) Longer-term experiments (months to years) that are ecologically relevant and incorporate realistic levels of natural variability	Managing cumulative impacts Resilience-based management
5) Determine capacity for acclimatization and adaptation to changing environmental conditions.*	Experiments targeting acclimatization and adaptation potential (e.g., parental effects, molecular mechanisms) Long-term, multigenerational studies Quantitative breeding designs	Prioritisation of species for protection Vulnerability assessments Interventions to support adaptation Understanding socio-economic implications
6) Determine how OA affects ecosystem function.	Experiments related to ecosystem function (e.g., food webs, trophic structures, predator-prey relationships, competition, recruitment) Establish links between laboratory experiments and the natural environment by combining laboratory experiments with field studies Continued support of mesocosm and field studies including natural CO_2 seeps Integrate experimental science with modelling to scale results and understand feedbacks	Understanding how ecosystems will respond. Identifying threshold values and management guidelines.
7) Identify the impacts of OA on reef-associated tourism and fisheries.*	Promote studies on ecologically and economically significant reef species Promote studies evaluating impacts on GBR-dependent people and industries	Supporting adaptation of industries and communities.
8) Assess the safety and cost-effectiveness of options to mitigate the impacts of OA on coral reefs.*	Evaluate feasibility and efficacy of intervention options through strategic scientific trials and cost-benefit analyses	Interventions to help mitigate OA Understanding cost-benefits, feasibility, efficacy, etc. of potential options

field studies. To assess ecosystem-scale effects of OA, we should continue to build on existing study systems, such as mesocosms and CO_2 seeps, while developing new strategies like integrated modelling and observational work (e.g., Albright et al., 2016).

7) What is the range of OA related impacts on reef-associated fisheries and tourism?

Our understanding of the impacts of OA on reef-dependent industries is limited. Studies are needed to assess the vulnerability of reef-dependent people and industries to OA, and on ecologically and economically significant species to interpret the socioeconomic implications of OA on fisheries and tourism. A better understanding of socioeconomic risks will allow managers to target efforts to help reef-dependent communities and businesses adapt (Marshall, 2010).

8) Are there safe, cost-effective options to mitigate the impacts of OA on the GBR?

Arguably the most critical knowledge gap is exploring options for human interventions aimed at reducing the impacts of OA. While further research addressing Priorities 1–7 is important, our knowledge of the implications of OA for coral reefs and associated goods and services is likely sufficient to warrant action. Care must be taken, however, to avoid risky interventions that have not been fully tested and examined. Experimental or pilot studies are needed to evaluate the feasibility and efficacy of various management options, particularly unconventional options that are largely untested such as selective breeding and geoengineering. A better understanding of their overall utility, limitations, costs, and the scales at which they may be effective, may prove useful as the condition of the world's coral reefs changes through time. Given the risks, care should be taken to adopt the precautionary principle and ensure that proposed interventions do not increase the likelihood of other adverse outcomes. Feasibility analyses also need to consider the global and long-term temporal scale of the OA problem – the anthropogenic CO_2 load will only diminish through neutralisation by sediment and rock dissolution and subduction at a time scale of thousands of years (IPCC AR5 WG1, 2013).

4.2. Research framework

We developed a strategic research framework to structure our thinking about the ways in which OA solution-focused research can be advanced to best support the development of management strategies (Fig. 3). While this framework was developed with the GBR and the GBRMPA in mind, it encompasses concepts that are broadly applicable to coral reefs worldwide and can be either used directly or adapted to other reef systems and their management objectives. The layers of the framework build upon each other, providing stepping stones that direct research into understanding OA impacts and addressing management needs. The first layer, 'exposure', encompasses research projects that strengthen our

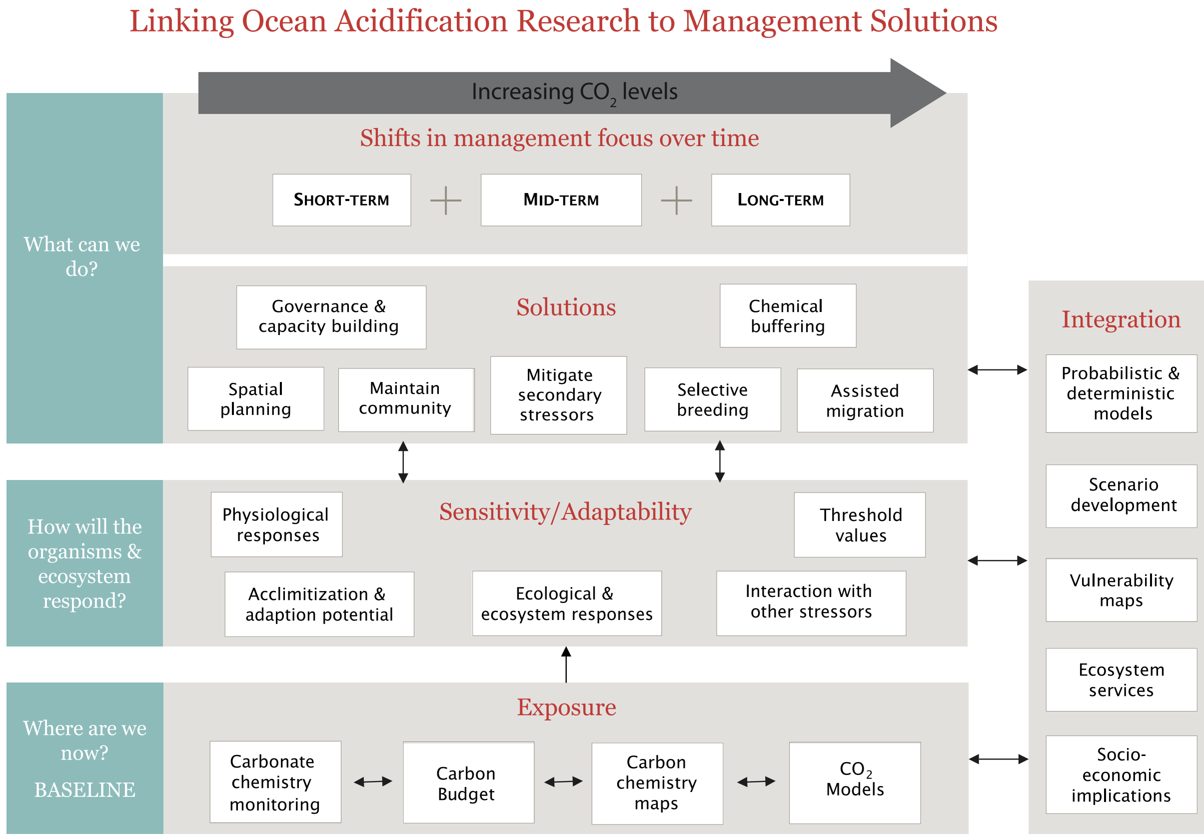

Fig. 3. Strategic research framework to link ocean acidification (OA) solutions-focused research to management solutions. The layers of the framework build upon each other to direct research into understanding OA impacts and addressing management needs for the GBR. Importantly, many of the suggested approaches should be addressed together as part of a comprehensive management strategy. See text for details (Section 4.2 – 'Research Framework').

baseline knowledge of carbonate chemistry, such as current levels of carbonate chemistry, spatial and temporal variability, and rates of change, so we can accurately assess current and projected levels of exposure to OA. Knowledge from this layer feeds into the 'sensitivity/adaptability' layer, which investigates how reef organisms and ecosystems respond to OA; research in this layer addresses impacts on fundamental biological and physiological processes including growth, reproduction, stress tolerance, adaptive capacity, etc. Scientific knowledge from the 'exposure' and 'sensitivity/adaptability' layers are combined in the 'integration' layer, which uses mapping techniques, modelling, and risk-assessment studies to explore interactions and feedbacks, fostering an ecosystem-level understanding of OA impacts on reefs and associated goods and services. The 'solutions' layer includes research that identifies options to assist organisms and ecosystems to respond to OA; research in this layer includes applied science that addresses the feasibility and efficacy of management options to further explore short- and long-term solutions to OA, ranging from spatial planning and ecosystem-based management to unproven strategies such as selective breeding and chemical buffering. The broader aim of the research framework is to understand the long-term and GBR-wide impacts of OA on social and ecological systems in the face of several cumulative stressors, and to assess which solutions are best applied today and in the future. The framework needs to be robust to a range of possible futures and should be adapted (jointly by scientists and managers) to continually re-evaluate key research priorities and management strategies. Importantly, the impacts of OA need to be assessed in combination with climate change, as OA chronically alters environmental conditions, and climate change results in both chronic (warming temperatures) and acute (increasing frequency of droughts and floods, potentially increasing intensity of tropical cyclones) impacts.

5. Conclusion

The intensity and diversity of stressors affecting the GBR, and coral reefs worldwide, continue to grow. In many ways, the GBR represents a best-case scenario for environmental management: robust governance of an iconic resource, with dedicated management and scientific resources. And yet, even in the case of the GBR, informed management decisions demand information that simply does not yet exist. Managers need the kinds of information we highlight here to sustain reef function into the future, and to deepen our understanding of long-term, ecosystem-level impacts of OA. Because none of the available approaches provide information on the full range of ecosystem responses, collaborative, targeted science is critical. Applying what we have learned at various levels of organization (i.e. molecular, cell, organism, and ecosystem) will facilitate a systems-level understanding of the projected condition of coral reefs as OA progresses. The final challenge is to understand how OA affects broader ecosystem level processes and how changes in our natural resources are likely to impact human livelihoods and our dependence on reef systems globally. Most importantly, we need to act on this information in a way that maximizes desired outcomes. The path forward is management supported by solution-based research that seeks to develop, trial, and refine pragmatic OA-mitigation strategies while also using them to fill knowledge gaps. Implementing regional responses may help curtail the continuing decline in ecological condition and value of the GBR, and reefs elsewhere, as we work towards the ultimate solution of mitigating global atmospheric CO_2 emissions.

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