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Preparing to manage coral reefs for ocean acidification: lessons from coral bleaching

Elizabeth Mcleod[1*], Kenneth RN Anthony[2], Andreas Andersson[3], Roger Beeden[4], Yimnang Golbuu[5], Joanie Kleypas[6], Kristy Kroeker[7], Derek Manzello[8,9], Rod V Salm[10], Heidi Schuttenberg[11], and Jennifer E Smith[3]

Ocean acidification is a direct consequence of increasing atmospheric carbon dioxide concentrations and is predicted to compromise the structure and function of coral reefs within this century. Research into the effects of ocean acidification on coral reefs has focused primarily on measuring and predicting changes in seawater carbon (C) chemistry and the biological and geochemical responses of reef organisms to such changes. To date, few ocean acidification studies have been designed to address conservation planning and management priorities. Here, we discuss how existing marine protected area design principles developed to address coral bleaching may be modified to address ocean acidification. We also identify five research priorities needed to incorporate ocean acidification into conservation planning and management: (1) establishing an ocean C chemistry baseline, (2) establishing ecological baselines, (3) determining species/habitat/community sensitivity to ocean acidification, (4) projecting changes in seawater carbonate chemistry, and (5) identifying potentially synergistic effects of multiple stressors.

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Acidification of ocean waters caused by increasing concentrations of carbon dioxide (CO_2) in the atmosphere is predicted to have dire consequences for calcifying organisms in the world's oceans during this century (Kleypas *et al.* 2006). Coral and coralline algal communities and the reef structures that they build are expected to be particularly vulnerable to ocean acidification (Silverman *et al.* 2009). Coralline algae are red algae that provide important ecological functions on coral reefs, including cementing carbonate fragments into reef structures, producing carbonate sediments, and providing settlement cues for reef-building coral larvae.

In a nutshell:

- Ocean acidification is likely to severely impact marine ecosystems, particularly coral reefs
- Conservation managers need information on the spatial and temporal variability of seawater carbonate chemistry and the sensitivity of marine organisms to ocean acidification for future planning and management
- This will enable lessons from conservation strategies aimed at coral bleaching to be applied to ocean acidification
- Ocean acidification research priorities must be established to guide coral reef conservation management and planning in a high carbon dioxide world

Ocean surface waters absorb about 25% of the CO_2 added to the atmosphere annually by human activities (Sabine *et al.* 2004; Le Quéré *et al.* 2009), lowering the pH level of seawater (Caldeira and Wickett 2003) and resulting in substantial changes in marine carbon (C) chemistry (Feely *et al.* 2004). Here, changes in C chemistry refer to shifts in the relative abundances of primarily three inorganic C species: CO_2, bicarbonate ions (HCO_3^-), and carbonate ions (CO_3^{2-}). Specifically, increasing atmospheric CO_2 leads to increasing seawater CO_2 (aqueous), HCO_3^-, and hydrogen ions (H^+), and decreasing CO_3^{2-} (Figure 1). The decline in the concentration of CO_3^{2-} reduces the seawater aragonite saturation state (Ω_a), which can lead to lower rates of reef calcification; aragonite is the mineral form of calcium carbonate ($CaCO_3$) deposited by corals (Kleypas and Langdon 2006; Andersson *et al.* 2009).

Managing for ocean acidification

To date, little attention has been given to specific management strategies that address ocean acidification (see Mcleod *et al.* 2008), beyond control of local stressors such as land-based sources of pollution and overfishing of marine herbivores (Anthony *et al.* 2011a; Kelly *et al.* 2011). This is because ocean acidification is often considered to be an insidious, global threat with unclear spatial patterns; coral reef managers therefore rarely consider it a feasible management target. Nevertheless, it is important to define how ocean acidification research can be applied

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[1]*The Nature Conservancy, Austin, TX* [*]*(emcleod@tnc.org);* [2]*Australian Institute of Marine Science, Townsville, Australia;* [3]*Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA;* [4]*Great Barrier Reef Marine Park Authority, Townsville, Australia;* [5]*Palau International Coral Reef Center, Koror, Palau;* [6]*National Center for Atmospheric Research, Boulder, CO;* [7]*Hopkins Marine Station, Stanford University, Pacific Grove, CA;* [8]*Cooperative Institute of Marine and Atmospheric Sciences, Rosenstiel School of Marine & Atmospheric Science, University of Miami, FL;* [9]*Atlantic Oceanographic and Meteorological Laboratory, NOAA, Miami, FL;* [10]*The Nature Conservancy, Honolulu, HI;* [11]*University of Aberdeen, Aberdeen, UK*

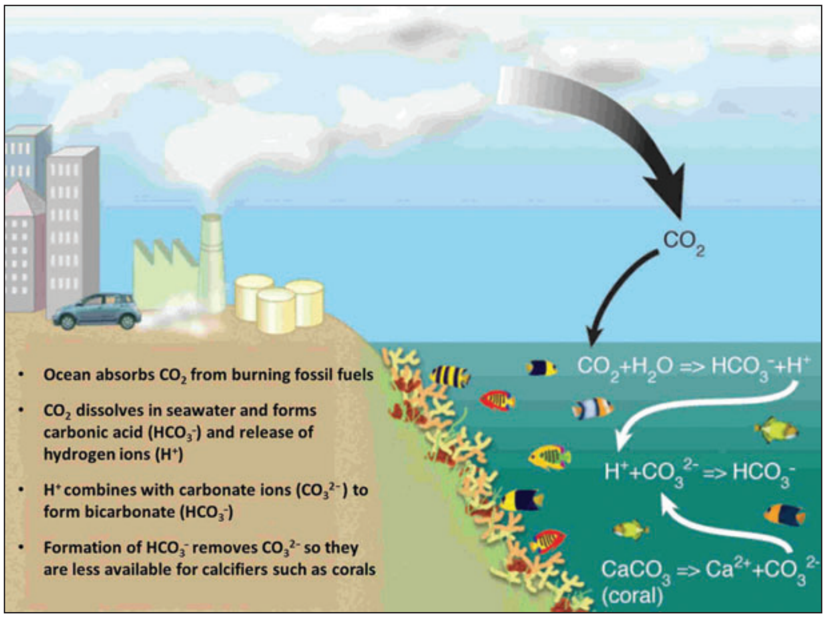

Figure 1. *Linkages between the buildup of atmospheric* CO_2 *from burning fossil fuels and the slowing of coral calcification due to ocean acidification. Atmospheric* CO_2 *is taken up by the oceans and results in a decrease in* CO_3^{2-} *concentration, making* CO_3^{2-} *unavailable to marine calcifiers like corals. (Modified from Hoegh-Guldberg* et al. *2007).*

to support conservation priorities. Coral reef managers faced a similar dilemma with coral bleaching; yet, over the past decade, conservation planning and management guidance has largely been developed to address the problem of coral bleaching and to support coral reef resilience (West and Salm 2003; Mcleod *et al.* 2009).

Ecosystem resilience refers to the ability of an ecosystem to maintain key functions and processes in the face of stresses or pressures (Holling 1973; Nyström and Folke 2001). Ocean acidification and warming (the latter a key driver of coral bleaching) are both results of increasing atmospheric CO_2, yet they have different stress characteristics and consequences for reef-ecosystem resilience. For example, bleaching episodes are typically caused by anomalous short-term warming events (lasting weeks to months) of water bodies of varying location and size (Berkelmans *et al.* 2004). Bleaching can result in increased coral mortality within months of the event and in local or regional reductions in coral growth and reproduction (Baird and Marshall 2002). By contrast, ocean acidification is a steady deterioration of the chemical conditions needed for physiological and biogeochemical performance of the reef ecosystem. The increasing frequency and intensity of coral bleaching events act as a mixed pulse- and press-type disturbance that directly affects reef health, as well as the capacity for reefs to recover between events. Ocean acidification is primarily a press-type stressor affecting recovery processes and lowering the resistance of corals to physical disturbances. However, in some cases, ocean acidification operates as a pulse disturbance (eg coastal marine ecosystems affected by seasonal upwelling of low-pH water or coastal zones affected by changes in nutrient delivery that impact carbonate chemistry; Feely *et al.* 2008; Borges and Gypens 2010).

Despite differences in the characteristics of bleaching and ocean acidification, several management approaches apply to both of these global stressors. Management approaches that support resistance and resilience to coral bleaching have only recently been implemented and have yet to be tested by major bleaching events, so their effectiveness cannot yet be determined for many coral reef areas. Recognizing this, we suggest three essential components to increase the coral reefs' ability to resist or recover from thermal stress: (1) spatial risk spreading, (2) management for maximum connectivity within networks of source and sink reefs ("source reefs" are net exporters of coral and fish larvae/eggs and produce enough larvae to maintain their home populations and may also supplement populations downstream, whereas "sink reefs" rely on larvae from reefs upstream), and (3) more vigilant management of local-scale stressors to enhance reef resilience (Panel 1). These same principles could also be applied to address ocean acidification, given that reefs impacted by this stressor are expected to be more vulnerable to coral bleaching (Anthony *et al.* 2008). Specific additional considerations for acidified reefs could include: (4) closely monitored management of herbivore fishing, as faster growing algae will be more likely to outcompete slower growing corals in acidified seas; (5) protection of reefs with low risk of exposure to storms, as coral growth and resilience will be reduced; and (6) marine protected area (MPA) designs that include shallow-water coral communities surrounded by seagrass beds to counteract local acidification (Anthony *et al.* 2011b).

Management strategies to address coral bleaching also focus on identifying local environmental factors that provide natural protection against bleaching; identifying and protecting coral species that are more resistant or better able to recover from thermal stress (eg based on different susceptibilities or acclimatization mechanisms); and using climate models to identify those reef areas with the highest probability of escaping the worst effects of warming (West and Salm 2003; Baker *et al.* 2008). Although their effectiveness requires further evaluation, these strategies provide a "bet hedging" approach, as coral reef communities most likely to survive climate-change impacts are identified and protected. To apply these approaches to ocean acidification, we argue that several research questions must be addressed. First, how do species, communities, and habitats vary in their sensitivity to changes in ocean chemistry? Second, what physical, chemical, or direct and indirect ecological factors affect their vulnerability? Third, what capacity do corals of different taxa have that would enable acclimatization or adaptation

Panel 1. Decision criteria used in conservation planning to address bleaching and ocean acidification

Planning criterion 1: protect natural refugia

Management actions can ameliorate conditions influencing bleaching severity and have been directed at identifying habitats and communities that are likely to be naturally protected from bleaching (West and Salm 2003). These "refugia" – areas more likely to survive disturbances – act as sources of coral larvae that reseed areas affected by bleaching. Refugia are therefore priorities for inclusion in marine protected areas (MPAs) (Mcleod *et al*. 2009).

Similarly, reefs that are likely to act as natural refugia as the oceans acidify include ecosystems that are less exposed or less sensitive to changes in seawater carbonate chemistry, reefs with high adaptive capacity to ocean acidification, and reefs where physical, chemical, or ecological factors can alleviate the impacts of ocean acidification. Such areas include reefs with physiologically resistant species (Fabricius *et al*. 2011) or locations projected to experience less change in seawater chemistry as oceans acidify (eg due to their ability to modify seawater chemistry; Anthony *et al*. 2011b). Coral communities that already experience naturally high fluctuations in pH or aragonite saturation state (Ω_a) could have adapted to these conditions, and might thus represent priorities for protection.

Planning criterion 2: maintain ecological connectivity among MPAs

Maintenance of ecological connectivity among MPAs is necessary to ensure that they are mutually replenishing, to facilitate recovery following a disturbance.

Ocean acidification has been shown to affect larval stages of marine organisms more so than adults (Kroeker *et al*. 2010), and has also been demonstrated to affect multiple stages of development and settlement in reef corals (Albright *et al*. 2010). Impacts on the larval stages ultimately affect connectivity, recruitment, and recovery, and are therefore important considerations for MPA design.

Planning criterion 3: protect replicates of major habitat types

Recognizing that climate change and ocean acidification impacts will not affect marine species equally everywhere (some marine organisms will even benefit), managers should build strategies for spreading the risk into MPA network design (Mcleod *et al*. 2009). To address coral bleaching, managers aim to protect multiple examples of the full range of marine habitat types in MPA networks (Salm *et al*. 2006).

Understanding how marine species and communities respond to variability in ocean C chemistry is still an active area of research. Because of the uncertainties regarding how marine species and communities will respond to ocean acidification, it will also be important to protect ecosystems likely to experience a variety of ocean chemistry patterns (eg high and low Ω_a, high variability of Ω_a).

Planning criterion 4: prioritize areas where local threats can be effectively managed

Management of local stressors (eg pollution, sedimentation, overfishing) can improve reef health and increase ecosystem resilience (McCook *et al*. 2007). Management actions (eg controlling overfishing of herbivores and land-based sources of pollution) can increase resilience to coral bleaching. For example, coral colonies experiencing higher local stress (effects of sedimentation, nutrients, human population, and fishing pressure) before 1998 were more severely affected by bleaching and recovered more slowly than those exposed to lower chronic stress (Carilli *et al*. 2009).

Management actions at a local scale are also likely to increase resilience to ocean acidification (Anthony *et al* 2011a; Kelly *et al*. 2011); these include controlling precipitation run-off and associated nutrient pollution, which can stimulate the growth of macroalgae, and pollutants, which can increase acidification in coastal waters. Furthermore, reducing fishing pressures on herbivore populations will promote control of macroalgae and favor coral and coralline algae, despite their slower growth rates under ocean acidification. Supporting ecosystem resilience in these ways will also help facilitate coral recovery after acute climate-change impacts (eg bleaching, disease, storms).

in response to changes in ocean chemistry? And finally, how will interactions between multiple stressors affect ecosystem resilience? Understanding how local, regional, and global factors can change the seawater C chemistry on coral reefs is a daunting challenge for coral reef managers. We tackle this issue below by proposing five priorities for ocean acidification research, targeted at guiding reef management and planning in a high CO_2 world.

Research priorities needed to integrate ocean acidification into conservation planning and management

Research priority 1: establish an ocean C chemistry baseline

Understanding the natural spatial and temporal variability of the seawater C system (ie CO_2, HCO_3^-, CO_3^{2-}, pH, and aragonite) on a given reef is important for assessing the sensitivity of a reef community to future changes in ocean chemistry. To characterize the potential threat that ocean acidification poses to a particular reef, researchers must account for the diurnal, seasonal, and climatological variability in the seawater C chemistry of a reef location or region for insight into the reefs' susceptibility to global changes in atmospheric CO_2. This is important because the seawater C chemistry, at any given point in time and space, is a direct function of the interaction between physical forcing (eg meteorology, oceanography) and diurnal/seasonal reef metabolism (Manzello 2010b).

Reefs experiencing high thermal variability may be more resistant to coral bleaching than adjacent reefs with less variability (McClanahan *et al*. 2007). In areas where it can be demonstrated that high variability in seawater pH and Ω_a confers increased resistance (eg via phenotypic plasticity) to ocean acidification, such places should be designated as priorities for protection. It could, how-

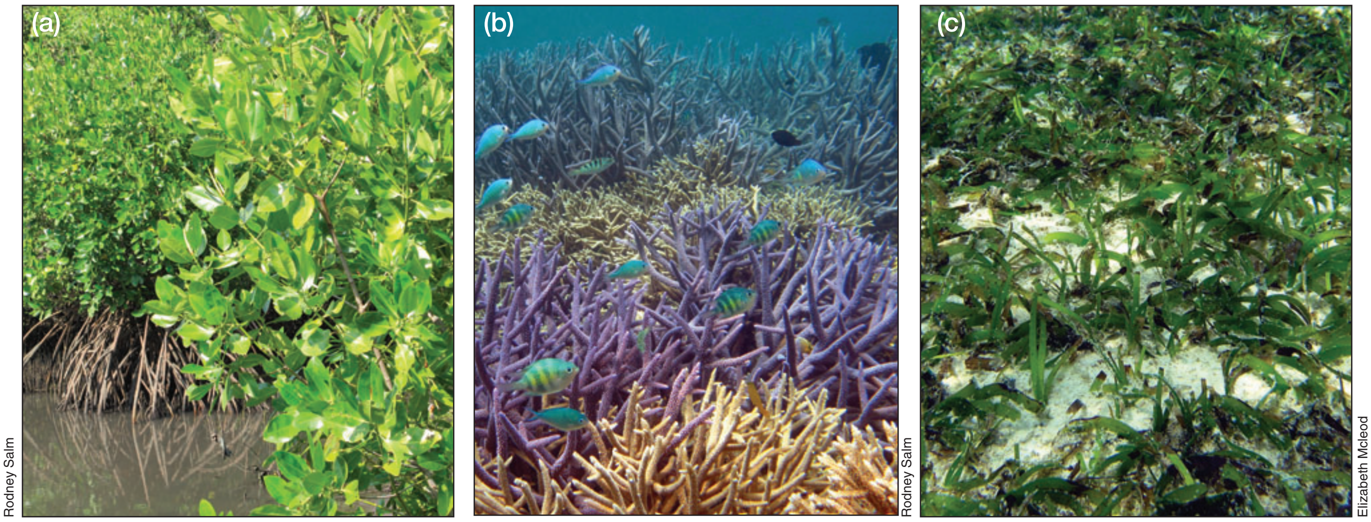

Figure 2. *(a) Mangroves, (b) coral reefs, and (c) seagrasses can substantially affect the seawater carbonate chemistry at local scales. Mangrove areas can experience very low seawater pH owing to decomposition of organic material (Millero* et al. *2001). Areas dominated by corals elevate* pCO_2 *(partial pressure of* CO_2*) and reduce* Ω_a*, thereby compounding ocean acidification effects in downstream habitats, whereas seagrasses may reduce* CO_2 *and elevate* Ω_a*, potentially offsetting ocean acidification impacts at local scales (Anthony* et al. *2011b).*

ever, be argued that areas exposed to more stable chemical conditions, such as oceanic reef fronts in areas that lack upwelling events, might be less vulnerable to ocean acidification, because it may take longer for these areas to experience the low pH values periodically observed in variable habitats. Importantly, given that natural variability in seawater chemistry can be substantial in places of prolific coral growth (Anthony *et al.* 2011b), understanding how this variability influences biological processes needs to be explored further.

Reefs that are currently experiencing high CO_2 and low pH and Ω_a (Manzello *et al.* 2008; Fabricius *et al.* 2011), or are situated in areas with high natural variability, and that have healthy coral and fish communities, may be naturally conditioned to low pH conditions and will therefore be potentially less vulnerable to ocean acidification. It will be important to assess the development of biological or ecological mechanisms to cope with or alleviate the impacts of high CO_2 conditions in these areas, or simply to understand the structure and function of reef communities with low Ω_a. Until our understanding of how local-scale and short-term C chemistry variation affects the biology of species and ecological communities, management strategies should include protection of ecosystems likely to experience a variety of ocean chemistry regimes (eg high and low Ω_a, high variability of Ω_a).

Research priority 2: establish ecological baselines

Conservation managers typically collect data on a variety of ecological characteristics, such as coral and benthic cover/composition; fish/invertebrate counts and size estimates; coral recruitment; fish spawning; and disturbance (eg bleaching, disease) and recovery. Such datasets provide useful information needed to understand coral reef health, but additional data are also needed to address reef resilience and vulnerability. These should include information about shifts in competitive interactions between corals and algae; changes in rates of growth, survivorship, and calcification of key reef-framework builders; likelihood of recruitment success; and changes in connectivity due to reduced larval survivorship (West and Salm 2003; Anthony *et al.* 2011a). Field studies that document changes in reef community structure and function over natural pH gradients are useful for identifying thresholds that trigger widespread ecological and biological changes. However, changes in growth, calcification, and the structure of reef communities are affected not only by ocean acidification but also by the many other human impacts affecting reefs globally, impacts that could potentially act synergistically with ocean acidification. Identifying how ocean acidification – in combination with other environmental and human-induced stressors – will affect ecosystem resilience will help to inform marine management decisions (Anthony *et al.* 2011a; Anthony and Maynard 2011).

To address the issue of reef vulnerability to ocean acidification, we need to identify which ecosystem attributes are the most relevant indicators of system state and the scale and frequency at which these attributes should be assessed. Such variables include benthic structural complexity, integrity or density of reef framework (eg abundance of $CaCO_3$ cements; Manzello *et al.* 2008), rates of coral and coralline algal calcification, and recruitment patterns of calcifiers. Additionally, it will be important to characterize the C chemistry of adjacent habitats (eg mangroves, seagrasses) and the ocean current patterns to and from these habitats, given that both biological and physical processes can influence the C chemistry on the reef (Figure 2; Panel 2).

Reef geomorphology and the spatial distribution of benthic habitat types can be used to assess the potential for local processes (eg habitat abundance patterns) to affect ocean acidification, which can be used to identify priority areas for conservation. For example, abundance patterns of corals, coralline algae, turfs, macroalgae, seagrasses, invertebrates, and sediment across reef zones provide proxies for how reef habitats drive natural patterns of water chemistry variation on reefs and thereby ameliorate or exacerbate ocean acidification impacts (Bates *et al*. 2010; Anthony *et al*. 2011b; Kleypas *et al*. 2011). This information can support a management framework that incorporates natural drivers of seawater C chemistry into MPA design.

Evidence suggests that some local-scale processes in shallow-water reef habitats may be more important in affecting changes in ocean chemistry than large-scale global changes (Panel 2; Bates *et al*. 2010; Anthony *et al*. 2011b). The C chemistry of reef waters varies strongly among reef zones (Suzuki and Kawahata 1999; Pelejero *et al*. 2005) and in many areas, major fluctuations in CO_2 and pH occur on diurnal to seasonal timescales (Bates *et al*. 2010; Manzello 2010b; Andersson and Mackenzie 2012). For instance, in some places, coral reef habitats may experience larger temporal (diurnal to fortnightly) and spatial variations in pH, pCO_2 (partial pressure of CO_2), and Ω_a than the mean projected changes for ocean waters during this century. Such local-scale processes may be greater than global changes in seawater C chemistry (Anthony *et al*. 2011b), although local-scale processes are ultimately affected by the C chemistry of the source water (ie of the open ocean) (Kleypas *et al*. 2011). Understanding the ability of a given reef system to buffer its own seawater C chemistry will have important implications for vulnerability to ocean acidification (Andersson and Mackenzie 2012). Changes in seawater C chemistry must therefore be assessed at the local reef scale, which is the scale at which management decisions are usually made.

Research priority 3: determine species, habitat, and community sensitivity

The calcification rates of coral and coralline algae vary in their sensitivity to ocean acidification (Anthony *et al*. 2008; Manzello 2010a; Fabricius *et al*., 2011). Sensitivity also varies within and across reef-building species, habitats, and communities. To identify areas that are least vulnerable to ocean acidification, managers will need to understand these differences and the interrelationships between them that help to reduce acidification impacts. For example, rates of coral calcification are projected to decline under ocean acidification, potentially leading to a decrease in coral resilience (Anthony *et al*. 2011a; Diaz-Pulido *et al*. 2011). Recent evidence also suggests that ocean acidification may affect fertilization and recruitment success (Albright *et al*. 2010), which has important implications for how source–sink relationships, connectivity, and recruitment potential are incorporated into MPA design.

The variation in coral susceptibility to temperature is now an important factor in reef management (as less sensitive reef species and communities can be prioritized for protection in MPAs); this approach can also be used as a basis for management approaches to ocean acidification. Coral sensitivity to bleaching varies across taxa and morphology (Baker *et al*. 2008). Similarly, the susceptibility of corals to ocean acidification also varies across taxa, at

Panel 2. Local factors that drive changes in seawater carbonate chemistry

In addition to the global drivers of ocean acidification (eg increasing atmospheric CO_2), local or regional processes can also buffer or potentially worsen ocean acidification.

Local factors include:

- ecological processes (eg photosynthesis, respiration, calcification, $CaCO_3$ dissolution)
- physical drivers (eg upwelling, water flow, bathymetry, residence time)
- human impacts in coastal waters (eg coastal pollution, eutrophication, overfishing of herbivores)

Several ecological and physiological processes taking place on a reef drive changes in the surrounding seawater carbonate chemistry. The relative contribution of photosynthesis (primary productivity), respiration, calcification, and $CaCO_3$ dissolution to the C budget of reef waters is largely a function of the composition of the benthic reef community (Anthony *et al*. 2011b; Kleypas *et al*. 2011). Understanding how the benthic community drives changes in carbonate chemistry on a reef and the connectivity of reefs to adjacent habitats (eg seagrasses upstream from corals, reefs in close proximity to mangroves) is essential for assessing reef vulnerability to ocean acidification.

An understanding of physical drivers (eg water flow, bathymetry, residence time) is also needed, to determine changes in seawater chemistry at the scale of coral reefs. The residence time of seawater in contact with each benthic community type is a key determinant of how upstream habitats can influence the seawater C chemistry of downstream habitats. For example, water on exposed outer reefs has negligible residence times; as a result, communities may be exposed to oceanic currents with more constant water chemistry and may therefore have less need to develop coping mechanisms to deal with chemical changes (Anthony *et al*. 2011a). By contrast, a reef enclosed in a bay or lagoon, which are likely to have long water residence times as exchanges with the ocean water may be restricted, may have developed higher resistance to ocean acidification because it regularly experiences low pH and Ω_a.

Human impacts in the coastal zone, such as nutrient and sediment loading, can exacerbate the impacts of ocean acidification. In some cases, coastal pollutants enriched with fertilizers can increase acidification, and land-use changes (eg in deforestation practices) can reduce direct and indirect CO_2 emissions and runoff (Kelly *et al*. 2011).

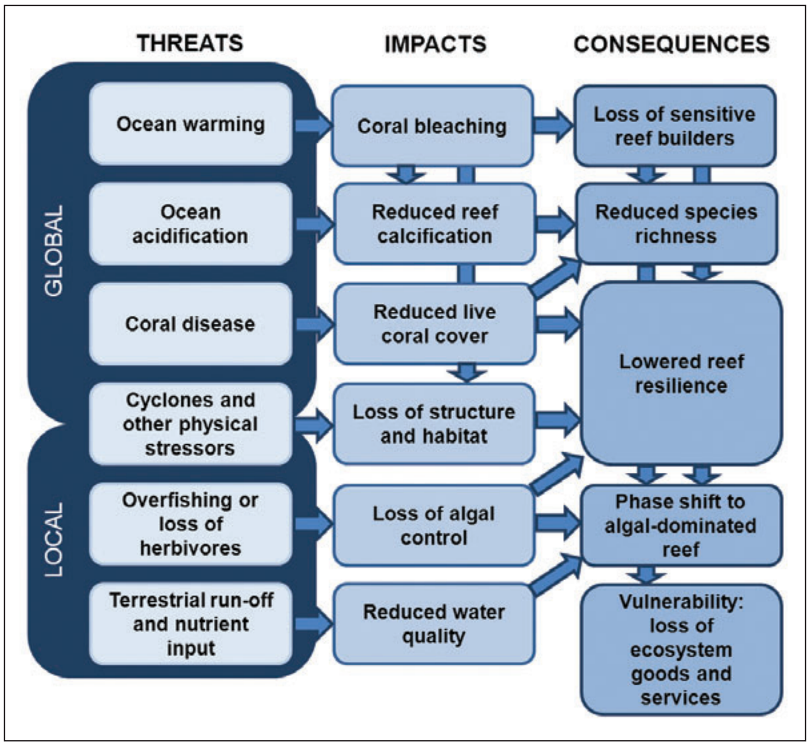

Figure 3*. Flow diagram of functional links between global and local threats to coral reef ecosystems, biological and ecological impacts, and downstream consequences for ecosystem function. Only a subset of the key links and interactions (arrows) are shown. (Modified from Anthony and Marshall 2009.)*

least in terms of the calcification response (eg Fabricius *et al.* 2011). To further complicate this issue, certain species demonstrate differing sensitivities to thermal stress and ocean acidification. For example, certain species (branching pocilloporid corals in Panama) have exhibited an increased tolerance to recurrent thermal stress events but appear susceptible to acidification, whereas other corals (massive pavonid corals in Panama) have exhibited greater vulnerability to thermal stress but may be less sensitive to acidification (Manzello 2010a).

Such information constitutes a challenge for managers who seek to identify and prioritize areas containing less vulnerable species, communities, and habitats for inclusion in MPAs. However, it is useful for predicting potential changes in species or habitat assemblages as a result of changes in ocean C chemistry.

Research priority 4: projecting changes in seawater C chemistry

To address the threat of ocean acidification, conservation managers need to assess ocean acidification risk within their conservation areas. This requires the ability to predict which reef areas are likely to experience the greatest or least changes in seawater C chemistry. Currently, projections for changes in ocean chemistry are only available at global and regional scales, through the use of general circulation models or biogeochemical box models (Andersson *et al.* 2005; Silverman *et al.* 2009). Assessments of large-scale patterns of ocean acidification often rely on an ensemble of coupled climate–C flux models (Caldeira and Wickett 2003) to help determine patterns of changes in pH, pCO_2, and Ω_a over the 21st century. Such approaches provide information to help assess the spatial and temporal distribution of ecosystem vulnerability to climate and ocean change at large basin scales (eg where Ω_a falls below the critical thresholds needed for coral calcification), but fail to capture and make projections about effects at the reef scale. Carbon chemistry is constrained by a handful of physical and chemical parameters (Zeebe and Wolf-Gladrow 2001), and thus model projections of seawater C chemistry (eg Caldeira and Wickett 2003; Orr *et al.* 2005) are generally robust at broad spatial and temporal scales of the open ocean (Blackford 2010). However, these projections have limited application in coastal regions because the models do not reproduce the high variability in CO_2, pH, and Ω_a due to benthic, land-based, or reef-associated processes in these areas (Panel 2). In coral reef environments, it is challenging to predict these conditions accurately, as reef processes (eg photosynthesis, respiration, calcification, dissolution) exert a strong control over the seawater C chemistry. Future coral reef seawater C chemistry will depend not only on the surrounding open ocean seawater chemistry but also on the local biological responses to these changes (Anthony *et al.* 2011b; Kleypas *et al.* 2011).

Research priority 5: identify potential synergistic effects of multiple stressors

Identification of the interactions and potentially synergistic effects of multiple stressors (eg sedimentation, other climate impacts, overfishing, excess nutrients, bleaching, cyclone impacts, coral disease, crown-of-thorns starfish [*Acanthaster planci*] outbreaks) is necessary to assess coral reef ecosystem resilience and, more specifically, vulnerability to ocean acidification. Conservation managers must contend with increasing ocean acidity in the context of other existing stressors (Figure 3). Research suggests that warming and changes in ocean chemistry can interact synergistically to affect photosynthesis, coral growth (Reynaud *et al.* 2003), and bleaching (Anthony *et al.* 2008). In a resilience context, the predicted increase in bleaching severity and frequency during coral bleaching events (Hoegh-Guldberg *et al.* 2007) enhances the need for rapid recovery between events. However, by slowing coral growth rates and increasing coral fragility to physical disturbances, ocean acidification further compromises recovery potential. Furthermore, ocean acidification has been shown to enhance the competitive advantage of macroalgae over corals (Diaz-Pulido *et al.* 2011), which may also have severe implications for reef resilience. Consequently, the combined roles of herbivore grazing (Mumby and Harborne 2010) and nutrient pollution (McCook *et al.* 2007) in the control of algal biomass and reef resilience become increasingly important as ocean acidity increases. Thus, overfishing, nutrient pollution, and ocean acidification could synergistically drive a transition to reefs dominated by macroalgae (Anthony and Maynard 2011). Managing the fishing of herbivores in areas that are identified as sensitive to ocean acidification can therefore be a useful local-scale approach to addressing acidification, as well as many other human impacts. There may also be instances where local resource use, such as seaweed mariculture, may favorably influence reef-level C chemistry.

Maps of exposure to multiple stressors (Maina *et al.* 2011) can provide information for decision support tools (eg MARXAN) that guide conservation planning. Such vulnerability maps, if extended to include ocean acidification for individual or groups of reef systems, could help conservation planners to manage for increasing atmospheric CO_2. Understanding how coral reefs will respond to changes in water chemistry through potential phase shifts (eg from coral to algal dominance) or through changes in calcification can provide important information to help identify priority areas for protection and conservation of coral reefs.

■ Conclusions

The Intergovernmental Panel on Climate Change (IPCC) projections for atmospheric CO_2 concentrations for the coming decades highlight the need for reef managers to address ecosystem vulnerability and resilience in their management and conservation strategies. Increasing global temperatures are already being considered (Mcleod *et al.* 2010), but it will be the combined consequences of temperature, ocean acidification, and other human pressures that will ultimately determine the future condition of coral reefs. By encouraging scientists to tackle ocean acidification research that specifically addresses conservation priorities, managers will be able (for the first time) to include ocean acidification exposure and risk into planning and management strategies.

Global atmospheric CO_2 emissions are currently exceeding those projected for the worst-case IPCC emissions scenario (Raupach *et al.* 2007). While stabilizing atmospheric CO_2 emissions is the most critical action needed to address ocean acidification, it is beyond the scope of on-the-ground conservation management. Innovative management strategies to enhance reef resilience and minimize exposure to increasing ocean acidity via spatial planning may provide partial protection for some reef areas. In addition to the research needs and management strategies outlined above, direct interventions that mitigate the impacts of ocean acidification (eg geo-engineering approaches) should also be considered. Although receiving little attention in the scientific literature, such approaches may represent viable options to support future conservation efforts at small scales.

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