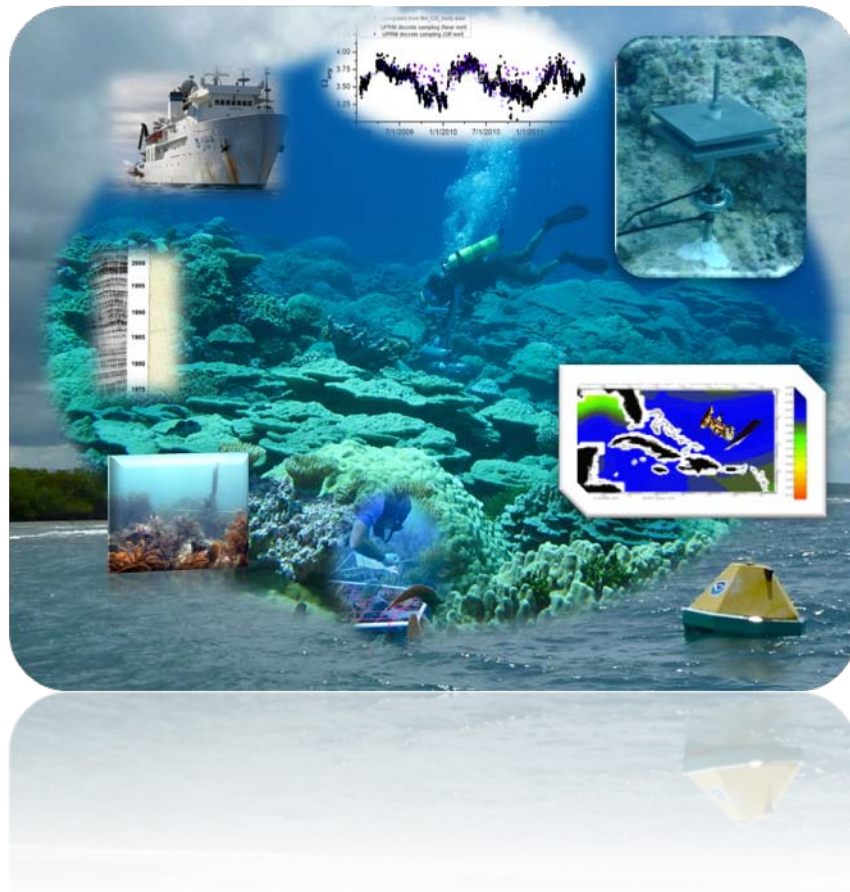


# Coral Reef Conservation Program Ocean Acidification Science Plan Fiscal Years 2012 - 2016



NOAA Technical Memorandum CRCP 18



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**FOR MORE INFORMATION:**

For more information about this plan or to request a copy, please contact NOAA's Coral Reef Conservation Program at 301-713-3155 or write to: NOAA Coral Reef Conservation Program; NOAA/NOS/OCRM; 1305 East West Highway; Silver Spring, MD 20910 or visit [www.coralreef.noaa.gov](http://www.coralreef.noaa.gov).

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# Coral Reef Conservation Program Ocean Acidification Science Plan Fiscal Years 2012 - 2016

D.K. Gledhill and J.D. Tomczuk (eds.)

National Oceanic and Atmospheric Administration

May 2012



## NOAA Technical Memorandum CRCP 18



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United States Department of  
Commerce

National Oceanic and  
Atmospheric Administration

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## Table of Contents

Acknowledgements.....	iii
Table of Contents.....	iv
Executive Summary.....	1
Introduction.....	2
Purpose.....	3
Authorities and Policy Drivers.....	4
Background.....	7
Part I: Inferring the Past.....	10
Part II: Observing the Present.....	14
Part III: Predicting the Future.....	18
Management and Decision Support.....	21
References.....	24

## Executive Summary

Changes in ocean chemistry in response to rising levels of atmospheric carbon dioxide, termed ocean acidification (OA), has emerged as a topic of considerable concern to scientist, policy makers, and resource managers. Over the next century changes in carbon dioxide could impart significant, albeit poorly understood, impacts to marine resources. The NOAA Coral Reef Conservation Program (CRCP) Ocean Acidification Science Plan is intended to guide NOAA funded coral reef ecosystem OA research for 2012-2016, including research conducted through extramural partners, grants and contracts. The plan covers all shallow coral reef ecosystems under the jurisdiction of the United States (U.S.) and Pacific Freely Associated States (PFAS), and outlines national research needed to address the many management challenges for reducing threats, reversing declines and promoting the resilience of coral reef ecosystems. The priority areas detailed in the plan are responsive to numerous legislative requirements including the Federal Ocean Acidification Research and Monitoring Act of 2009 (Public Law 111-11) and the National Ocean Policy Executive Order (July 2010), and align with broader NOAA strategic documents including the *NOAA Ocean and Great Lakes Acidification Research Plan* and the *NOAA Next Generation Strategic Plan*.

The research priorities identified in the plan are designed to address the following three questions.

- What recent past declines in coral reef ecosystems health can be attributed to OA?
- What present aspects of contemporary coral reef ecosystems are most susceptible to OA?
- What are the future effects of OA together with other global and local threats in this century on coral reef ecosystems?

## Introduction

Coral reef ecosystems provide a wide range of biological, ecological, cultural, and economic resources valued worldwide at approximately \$30 billion annually (Cesar et al., 2003). The goods and services provided by coral reef ecosystems include renewable and non-renewable resources, coastline protection, increased property values, tourism, habitat for important fisheries species, cultural value, and marine natural products. Coral reef ecosystems have undergone significant declines in overall condition in recent decades and are considered under threat from a multitude of natural and anthropogenic stressors including unsustainable fishing practices, land-based sources of pollution, and a changing climate.

Atmospheric carbon dioxide concentrations, driven in large part by human activities (i.e., carbon energy demands and changes in land use), have now reached levels greater than, and are increasing at a rate faster than experienced for 55 million years (Pearson and Palmer, 2000). The global oceans act as the largest natural reservoir for this excess carbon dioxide, currently absorbing about a third of that associated with human activities each year. As carbon dioxide reacts with seawater it fundamentally changes the chemical environment through a process termed “ocean acidification”. These changes include not only reducing pH (hence the term “acidification”), but also change the availability of a range of chemical carbon compounds that are tightly linked with biological processes including productivity, respiration, and calcification. These changes will likely alter biological processes and fundamentally change the composition of carbonate marine sediments and substrates that are composed of calcium carbonate minerals and serve as important building blocks for coral reef ecosystems.



*Figure 1. A primary driver of ocean acidification is societies continued rising demand for carbon-based energy sources where the unmitigated byproduct (carbon dioxide) transfers carbon from the geologic reservoirs into the atmospheric.*

## Purpose

Global change related stressors to coral reef ecosystems do not always rank as key priorities with local management given the perceived limited influence in mitigating the effects at local levels. However, central to NOAA's mission is a requirement to evaluate, monitor and forecast the effects of large scale processes on the Nation's marine resources. To achieve this mission requirement, the CRCP intends to establish OA relevant national status and trends and devise local, regional, and national management strategies.

The CRCP Ocean Acidification Science Plan outlines priorities to understand the potential consequences of OA on coral reef ecosystems and to facilitate management of the coral reef ecosystems under the jurisdictions of the U.S. and PFAS. The priorities in the plan are comprised of a broad range of research, status and trends monitoring, modeling, and decision support tools. The plan is intended to align with the CRCP Goals and Objectives 2010-2015 and other NOAA Research and Strategic Plans to minimize duplicative investments, and where appropriate promote the development of complimentary activities with NOAA programs and external partners.

NOAA exhibits the capacity to provide for sustained long-term monitoring, process investigations, manipulative experiments, and diagnostic and forecast modeling, but also relies on external research partners to complement and augment these capabilities. While this plan is intended to primarily address research priorities in the short-term 2012–2016, it also sets the stage for mid to long-term efforts that require sustained observations to allow for rigorously quantifying changes and understanding the processes and rates of OA impacts to coral reef ecosystems.



## Authorities and Policy Drivers

The authorities and policy drivers (e.g., legal mandates, executive orders, and treaties) for conducting the activities detailed in this plan are as follows:

### **AUTHORITIES**

#### **Primary**

- Coral Reef Conservation Act (16 U.S.C. 6401 et seq.)
- Executive Order 13089: Coral Reef Protection (1998)
- Federal Ocean Acidification Research and Monitoring Act of 2009 (Public Law 111-11)
- Magnuson-Stevens Fishery Conservation and Management Act (16 U.S.C. 1801 et seq.) as amended by the 2006 Magnuson-Stevens Reauthorization Act (Public Law 109-479)
- U.S. National Ocean Policy Executive Order (July 2010)
- Endangered Species Act (16 U.S.C. 460 et seq.)

#### **Secondary**

- Coastal Zone Management Act (16 U.S.C. 1451 et seq.)
- Government Result and Performance Act of 1993 (31 U.S.C. 1115 et seq.)
- Marine Mammal Protection Act (16 U.S.C. 1361 et seq.)
- National Environmental Policy Act (42 U.S.C. 4321 et seq.)
- National Marine Sanctuaries Act (16 U.S.C. 1431 et seq.)
- NOAA Undersea Research Program Act of 2009 (Public Law 111-11)
- Presidential Proclamation 8031: Establishment of the Northwestern Hawaiian Islands Marine National Monument (2006)
- Presidential Proclamations 8335, 8337, and 8336: Establishment of the Marianas Trench, Pacific Remote Islands, and Rose Atoll Marine National Monuments (2009)

## **POLICY DRIVERS**

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NOAA's Mission is to understand and anticipate changes in climate, weather, oceans, and coasts; share that knowledge and information with others; and to conserve and manage marine resources. NOAA generates tremendous value for the nation – and the world – through its longstanding mission of science, service, and stewardship by advancing our understanding of and anticipating changes in the Earth's environment; by improving society's ability to make scientifically informed decisions; and by conserving and managing ocean and coastal resources.

The priority research needs of this Plan are directly related to the following NOAA drivers:

NOAA's Next Generation Strategic Plan (NGSP) Climate Adaptation and Mitigation Goal:

- A key objective towards achieving NOAA's long-term goal of an informed society that anticipates and responds to climate and its impacts is acquiring an improved scientific understanding of the changing climate system and its impacts.

NOAA's NGSP Healthy Oceans Goal:

- The goal is marine fisheries, habitats, and biodiversity sustained within healthy and productive ecosystems. It identifies the need for an improved understanding of how OA will alter habitats and the relative abundance and distribution of species, as well as the productivity of coastal and marine ecosystems, affecting recreational, economic and conservation activities.

NOAA's NGSP Resilient Coastal Communities and Economies Goal:

- This goal recognizes that the interdependence of ecosystems and economies makes coastal communities increasingly vulnerable to impacts of climate change and other hazards. Strategies to improve coastal resilience to these hazards include equipping coastal decision makers with science-based information, tools and technologies and management strategies related to adaptation, risk communication, hazard response and recovery and resource conservation to effectively reduce climate change impacts to communities and their economies.

NOAA's NGSP Enterprise Objective - holistic understanding of the earth system through research:

- Progress towards this objective includes understanding and characterizing the role of the oceans in climate change and variability; and the effects of climate change on the ocean and coasts, including biological, chemical, and geophysical effects (e.g., sea level rise, OA, and living marine resources).

NOAA's Ocean and Great Lakes Acidification Research Plan (NOAA OA National Plan):

- The Plan details NOAA requirements to characterize the biogeochemical changes across a range of environments, evaluating the response of key aquatic organisms and ecosystems, and identifying the range of vulnerabilities in order to inform adaptive management strategies.

NOAA's CRCP Goals and Objectives: 2010-2015

- The CRCP goals to address climate change and ocean acidification include to identify, understand, and communicate risks and vulnerabilities confronting U.S. coral reef ecosystems, ecosystem services, and dependent human communities associated with climate change and OA, and to foster and understand coral reef ecosystems through improved and applied understanding, forecasting, and projecting of climate change and OA impacts.

## Why is ocean acidification a concern for coral reef ecosystems?

Coral reef-building organisms construct vital habitat for associated biota in addition to providing protection to coastal human populations through dissipation of wave energy (Lugo-Fernandez et al., 1998; Gratwicke and Spieght, 2005). Any decline in net calcification by coral reef organisms could compromise long-term persistence of many coral reef ecosystems because growth of healthy, undisturbed coral reefs are known to only slightly outpace rates of loss due to physical and biological erosion (Glynn, 1997).

The ability of coral reefs to maintain adequate calcification under increased OA remains a primary concern since a number of laboratory studies have measured reduced rates of calcification for many species of reef building coral under expected OA conditions (Gattuso et al., 1998; Marubini et al., 2001, 2002; Marshall and Clode, 2002; Ohde and Hossain, 2004; Borowitzka, 1981; Gao et al., 1993; Langdon et al., 2000, 2003; Langdon and Atkinson, 2005; Leclercq et al., 2000, 2002; Anthony et al., 2008). Still, others have shown a more subdued and complex response (Ries et al., 2010; Reynaud et al., 2003; Ries et al., 2009; Jury et al., 2009; Cohen et al., 2009; Rodolfo-Metalpa et al., 2010; Holcomb et al., 2010) precluding any simple narrative to how OA will impact coral calcification rates.

- Composed predominantly of scleractinian corals
- High biodiversity (600,000 to 9 million reef species)
- Structural complexity drives biodiversity

microscopic algae

coral polyps

Calcium carbonate skeleton  $CaCO_3$

$$Ca^{2+} + CO_3^{2-} \rightarrow CaCO_3$$
$$\Omega_{\text{phase}} = \frac{[Ca^{2+}][CO_3^{2-}]}{K_{\text{sp, phase}}}$$

"Saturation State"

*Saturation State ( $\Omega$ ): For corals, the carbonate mineral which comprises much of the skeletal structures is often aragonite. The degree to which seawater is supersaturated with respect to aragonite is reported as the 'saturation state' denoted as  $\Omega_{\text{arg}}$ . Based on purely physical chemistry, where  $\Omega_{\text{arg}}$  is greater than 1, precipitation is favored and dissolution can occur when  $\Omega_{\text{arg}}$  is less than 1.*

While the precise mechanism remains a matter of considerable debate, studies where the reduction in calcification rates were observed have typically been interpreted as a response to variations in the degree to which seawater is supersaturated with the carbonate minerals that comprise many marine organisms skeletal and shell structures. Such responses suggest calcification rates have likely declined since the pre-industrial period given the reduction in carbonate minerals that has transpired. Some recent coral growth studies have suggested that coral calcification and extension rates have declined 14-24% on the Great Barrier Reef, the Red Sea, and in southern Thailand since approximately 1990, in part due to rising sea surface

temperatures. However, the contributing influence of OA still remains ill defined (Cooper et al., 2008; Lough, 2008; De'ath et al., 2009; Tanzil et al., 2009; Cantin et al. 2010). Significant declines in growth rates of Caribbean corals have also been documented (Edmunds, 2007; Bak et al., 2009), but clearly result from a combination of local and global changes and the specific effects of OA are difficult to discern. In fact, while a recent study of *Montastraea faveolata* from the Florida Keys did find a decrease in density over the period 1937 and 1996, no such decline was apparent in extension or calcification (Helmle et al., 2011). This may suggest some species exhibit a natural tolerance or local environmental conditions can compensate for global OA effects.

Beyond the potential direct effects for coral calcification, OA poses additional concerns for coral reef ecosystems. This includes dissolution of coral reef sediments which often contain appreciable amounts of more soluble carbonate minerals (Morse et al., 2006). Sediment dissolution may outpace carbonate production on many coral reefs by 2030 (Yates and Halley, 2006). OA may compromise coral reef framework integrity and resilience in the face of other acute threats such as coral bleaching, diseases, increases in storm intensity, and rising sea level (Silverman et al., 2009). Indeed, in carbon dioxide enriched waters off the Galapagos Islands, coral reef structures were completely eroded to rubble and sand in less than 10 years following the acute warming disturbance of the 1982-1983 El Niño event (Manzello, 2009).

Other expected impacts of OA include a potential lowering of the thermal thresholds for bleaching (Anthony et al., 2008), impairment on early life stages of corals such as reduced fertilization success, reduced larval settlement, and reduced growth and survival rates of newly settled corals (Albright et al., 2008; Cohen and Holcomb, 2009; Albright et al., 2010, Morita et al., 2010; Suwa et al., 2010). These species level impacts are particularly relevant given the potential extension of Endangered Species Act protection for additional scleractinian coral reef species. The Act grants conservation actions for species at risk of extinction.

Direct impacts of OA on coral growth and fitness, in combination with largely unknown potential impacts on non-calcareous competing functional groups, may profoundly affect the basic ecological interactions that structure coral reef ecosystems. This may provide even greater challenges for local management strategies aimed at retaining or regaining coral reefs. A recent meta-analysis of available experimental data suggests that such “phase shifts” might increase in response to OA. Specifically, as calcification is reduced, algae (non-calcifying) and sea grass may benefit (Hendriks et al., 2010). The affects of OA on some non-calcifying organisms may indeed be just as serious as the affects to calcifiers, but are largely unexplored. It is known that OA can impair the olfactory senses in larval clownfish that are used by juveniles to locate suitable habitat (Munday et al. 2009). It is also important to note, that other species of fish, as well as certain corals, may be less sensitive to OA (Ries et al. 2009; Munday et al. 2011). Given the paucity of experimental manipulations, field studies, and understanding regarding the fundamental carbonate chemistry dynamics and species sensitivities to OA, it is premature to suggest a broad consensus conclusion regarding the ultimate fate of coral reef ecosystems in response to OA.

Finally, while coral reef ecosystems are considered the most biologically diverse of all marine ecosystems, the diversity varies greatly across spatial and environmental gradients. How this variation influences coral reef ecosystem resilience and adaptation to climate change and OA is poorly understood. Much of the biomass and biodiversity of coral reef ecosystems lies in the complex architecture of the coral reef matrix (Ginsburg, 1983; Small et al., 1998; Sala and Knowlton, 2006; Knowlton et al., 2010). The potential impacts of OA on this community of organisms, collectively known as the cryptobiota (Macintyre et al., 1982), remains largely unknown. In addition, predictions of coral reef ecosystem responses to OA are further complicated due to the fact that coral reef organisms secrete species specific types of calcium carbonate mineralogies (i.e., aragonite, calcite, and magnesium calcite) which exhibit a range of solubilities. Understanding the biodiversity and community structure of coral reef ecosystems is therefore a necessary step to recognize and predict shifts in ecosystem structure due to OA impacts.

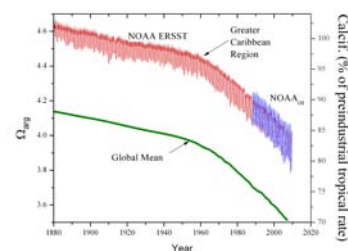
## Priority Research Activities

The Plan's priority research activities are intended to identify and integrate with management needs to facilitate stewardship of coral reef ecosystems under the jurisdictions of the U.S. and PFAS. Research activities gaps include establishing a historical context of OA impacts, understanding coral reef ecosystem susceptibility to OA and forecasting the effects of OA in the future. Outcomes of these activities are an important step for developing local management actions to foster enhanced resilience for coral reef ecosystems under a changing climate and ocean chemistry.

### Inferring the past: establishing a historical context of ocean acidification impacts

#### Description of the Problem:

While the rate of OA is currently accelerating in most regions of the ocean, it is not a new phenomenon. Anthropogenically driven OA has occurred since at least the industrial revolution albeit at a slower rate than present. The changes that have occurred in coral reef ecosystem conditions over the past 100 years need to be re-evaluated to better account for our understanding of their sensitivity to changes from OA. Additional information is needed to construct past events and develop historical baselines that can serve to track future changes and identify specific regions and/or organisms naturally resilient to OA.



*Figure 2. Changes in surface ocean aragonite saturation state from the Ocean Acidification Product Suite v0.3 model in the Greater Caribbean Region should have yielded a 15% decline in coral calcification rates based upon laboratory estimates (Gledhill et al., 2010).*

#### Task 1.1: What are the past rates and magnitude of ocean acidification?

**Approach: Improved constraint on the rates and magnitude of ocean acidification at both regional and local-scales.**

For more than a decade, direct measurements of ocean chemistry via ship surveys, long-term time series stations, and autonomous moored and underway platforms have been used to track changes in ocean chemistry. There remains a requirement to synthesize these historical measurements aided by the application of satellite remote sensing and synoptic models to provide for regionally specific characterization of changes in ocean chemistry extending back several decades. While this approach is valuable to provide a regional context to the changes from OA, the products developed in most cases will be limited because the information cannot necessarily reveal the local chemical changes occurring in coral reef ecosystems. Instead, new techniques such as geochemical techniques should be explored (e.g., boron-based pH estimates) to aid in establishing past chemical changes in coral reef ecosystems. Geochemical techniques are still largely in the development phase and careful calibration and validation



studies should commence prior to incorporating geochemical techniques for operational monitoring.

### **Task 1.2: How have coral reef ecosystems historically responded to ocean acidification?**

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#### **Approach: Quantify past ocean acidification changes in coral calcification rates.**

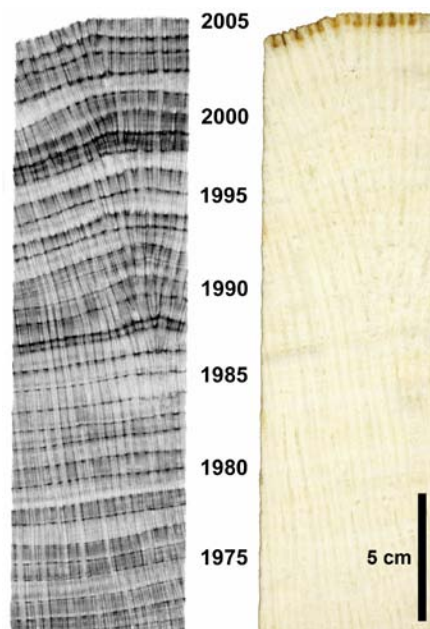
There are a broad range of changes that may have transpired from historical OA including changes in larval recruitment, biodiversity, bioerosion rates, and calcification rates and many of these changes are difficult to quantify in hindcast. However, corals do provide a unique recorder of growth rates by means of depositing calcium carbonate (aragonite) skeletons in distinct growth bands and can grow for several hundred years. Similar in approach to counting the rings of a tree to assess growth patterns, cyclic variations in skeletal porosity produce annual density bands that provide a record of coral growth rates. Through the application of coral sclerochronology, historical growth records can be gathered from some species of branching and massive coral reef building scleractinians. X-radiograph densitometry techniques can be applied using x-ray imaging of sectioned coral cores (Figure 3) to examine the growth rates and calcification rates (Helmle et al., 2011).

Also, a range of other techniques are currently available including the use of CAT scan images to determine the three-dimensional internal structure and annual banding (Cohen et al., 2009; Saenger et al., 2009) of both cores from massive corals and samples of branching corals. Studies using these techniques can provide valuable insight into the history of a coral's growth rate (e.g., skeletal linear extension, bulk density, and calcification) and the associated response to long-term environmental changes such as OA particularly when conducting in tandem with Task 1.1. The information collected from the growth rate records can then be compared against regional and local changes in carbonate chemistry to evaluate if past changes in coral growth are consistent with the expected OA responses demonstrated in laboratory based experiments and whether certain coral reef locations exhibit increased susceptibility or resilience.

#### *Priority Research Locations:*

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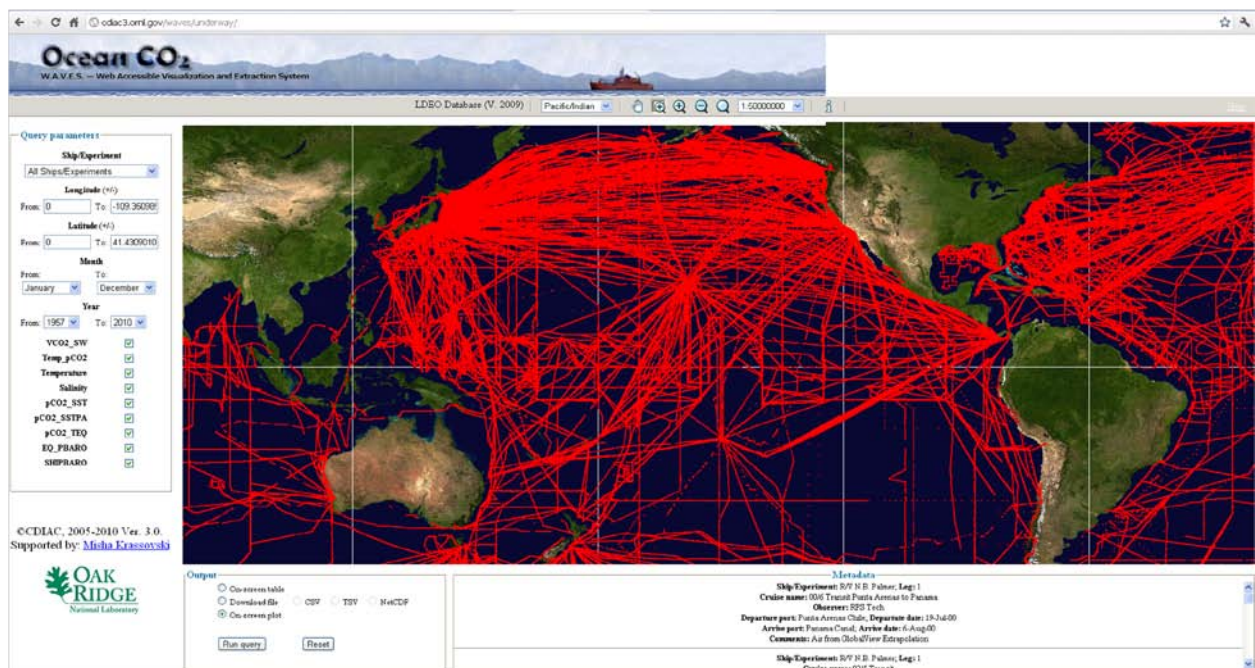
Develop regionally specific synthesis products that describe the historical changes in surface ocean chemistry for Pacific and Atlantic U.S. coral reef ecosystems. NOAA laboratories (Pacific



*Figure 3. Shows an x-ray imaged coral core. The left image in black and white shows a positive print with annual density bands (dark bands = high density and light bands = low density). The right image is a photograph of the coral slab (Helmle and Dodge, 2011).*



Marine Environmental Laboratory (PMEL), and Atlantic Oceanographic and Meteorological Laboratory (AOML) have acquired surface ocean carbon data for more than a decade in both the Pacific and Atlantic Ocean basins and marginal seas as part of ongoing efforts to monitor the uptake of anthropogenic carbon dioxide by the oceans. Regional carbon monitoring efforts relevant to U.S. coral reef ecosystems in the Greater Caribbean region have benefited from volunteer observing ships outfitted with systems that measure the partial pressure of carbon dioxide in seawater deployed by NOAA. The datasets serve as the basis for the development of the NOAA Coral Reef Watch Experimental Ocean Acidification Product Suite (OAPS) which uses satellite and synoptic environmental datasets to scale up these observations to produce monthly estimates of surface ocean carbonate chemistry.



*Figure 4. A subset of historical ship tracks obtained from Carbon Dioxide Information Analysis Center where surface carbonate chemistry is collected as part of ongoing survey efforts in both ocean basins by NOAA and international partners.*

Additional datasets can be obtained from the Carbon Dioxide Information Analysis Center and tailored to develop regionally specific products similar to OAPS described above for the Pacific and Atlantic Ocean basins.

While the Pacific surface waters are naturally less saturated with carbonate minerals, the Atlantic/Caribbean waters have likely experienced a greater rate and magnitude of change historically. This implies a need to characterize historical changes in coral growth and near reef carbonate chemistry in order to understand the impacts of OA over the industrial period. Where possible, efforts should work in conjunction with established ongoing monitoring and process investigations studies such as the Atlantic OA Test-bed locations (e.g., La Parguera, Puerto Rico and the Cheeca Rocks Complex in the Florida Keys National Marine Sanctuary). This does not preclude the need for efforts to catalog growth rates in the Pacific and indeed there are ongoing efforts to measure historical growth rates in the remote Pacific islands. While the

remote Pacific Islands ecosystems may not have experienced as significant a change in response to OA thus far, they do represent ecosystems where global environmental change (e.g., OA and temperature) may have been the dominant agent of stress historically, thereby making it more readily discernable relative to the highly impacted Atlantic systems.

*Expected Outcome:*

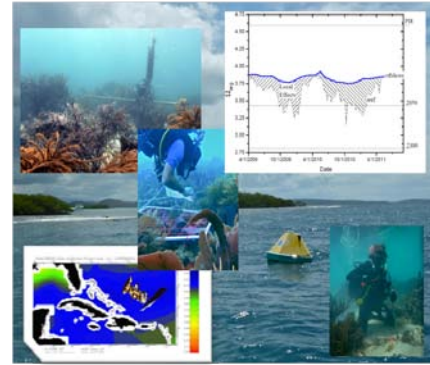
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Efforts will develop a historical baseline of OA in each of the basins for U.S. coral reef ecosystems. Regional synthesis products should focus on detailing the historical trends and dynamics of OA and provide assessments of coral extension, density, and calcification over the last several hundred years to identify potential historical impacts of OA prior to and following the industrial revolution. The assessments of both changing ocean chemistry and historical growth rates should reveal a range of sensitivities of different coral reef ecosystems to global environmental change and will assist in identifying areas of concern.

## Observing the Present: Understanding contemporary coral reef ecosystems susceptibility to ocean acidification

### Description of the Problem:

Coral reefs comprise a mosaic of habitats dominated by different substrate types (i.e., coral-dominated, coralline algae-dominated, macroalgae dominated, reef rubble, reef sediments, bare rock, seagrass beds, and sand flats), that are likely to respond different to OA. Within tropical surface ocean (non-coastal) waters, the annual changes in regional ocean chemistry due to OA can be roughly estimated from the assumption that surface water carbon dioxide tracks atmospheric concentrations on an annual basis (Orr et al., 2005; Bates, 2007). However, at finer scales other processes including changes in temperature and salinity (Gledhill et al., 2008), upwelling (Manzello et al., 2008, Feely et al., 2008), physiological processes (e.g., photosynthesis, respiration, and calcification) (Salisbury et al., 2008, Keul et al., 2010), and carbonate production (Balch et al., 2009), play important roles on regulating the carbonate chemistry. All of these factors can potentially influence the rates and magnitude of chemical change in coral reef ecosystem waters. Understanding the complexity of local carbonate chemistry dynamics across multiple temporal and spatial scales is a critical need. This complexity is likely to yield a range of coral reef susceptibilities to OA which, if adequately modeled, can be employed in the development of cumulative impacts models (Selkoe et al., 2008) and inform long-term management strategies.



*Figure 5. The Atlantic Ocean Acidification Test-bed unites a number of observing capabilities with process investigations.*

### Task 2.1: What is the natural variability in coral reef carbonate chemistry and how is it changing?

#### Approach: Establish coral reef ocean acidification observing capabilities.

A coordinated and targeted series of field observations, moored autonomous deployments and modeling efforts are needed to document the dynamics of OA in coral reef ecosystems. The observing and monitoring capabilities should incorporate processes studies, promote model development, and leverage other federal and academic investments when possible. One strategy the CRCP is developing as part of its National Coral Reef Monitoring Plan will couple discrete water chemistry collections to moored observatories (see insert). This carbonate chemistry monitoring strategy includes broadly distributed spatial water sampling surveys complemented by a more limited number of moored instruments rotated among a small subset of representative sites in both the Atlantic/Caribbean and Pacific regions.

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### **National Coral Reef Ecosystem Monitoring Plan**

NOAA's CRCP is developing a long-term National Coral Reef Monitoring Plan (NCRMP) that will focus on four core variables (coral/benthos, fish, climate, and human dimensions) to measure long-term across coral reef ecosystems in CRCP priority geographic areas, and integrated to assess status and trends in a periodic national level report. While the overall strategic planning for monitoring is ongoing, the NCRMP climate strategy identified the need to monitor physio-chemical status and trends for U.S. coral reef ecosystems and includes the following aspects:

Discrete Sampling: Activities will include discrete water sampling for carbonate chemistry measurements to characterize the spatial heterogeneity of carbonate chemistry across a diverse set of coral reef ecosystems. The sampling will provide insight into the spatial dynamics of local carbonate chemistry interpreted in the context of the broader regional changes. At a select subset of locations, this short-term variability will be further refined through repeated sampling across diel cycles aided by autonomous water samplers.

Autonomous Time-Series: A limited number of moored instruments will be deployed at select sites in the Atlantic/Caribbean and Pacific basins. At a minimum, these moored instruments will provide sustained autonomous measurements of temperature, salinity, and carbon dioxide partial pressure and be co-located with other CRCP biological and climate status and trends monitoring activities. The sites with instruments will provide process level monitoring to determine the primary controls on local carbonate chemistry dynamics (Gattuso et al., 1997; Anthony et al., 2011) and monitor community response to OA impacts.

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### **Task 2.2: How do coral reef communities differ amongst the natural variability in carbonate chemistry and how are they changing in response to ocean acidification?**

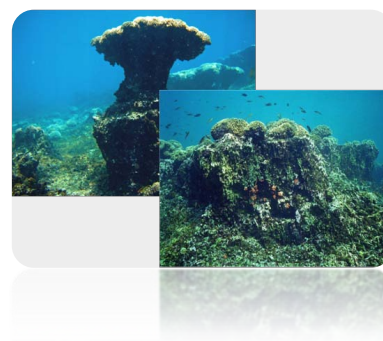
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**Approach: Characterize and track changes to the natural distribution of coral reef biodiversity and key functional processes likely to be impacted by ocean acidification.**

An anticipated impact of OA to coral reef ecosystems is a change in the net carbonate budget (e.g., building versus loss). Yet few methods exist to routinely monitor broad scale changes in overall coral reef budgets. Development of methods that couple both satellite remote sensing (e.g., hyperspectral habitat characterizations) and *in situ* monitoring tied to process investigations have been proposed that might capture shifts in carbonate budgets over long-term time-scales. However, achieving this in the near term by 2016 is likely unrealistic given fiscal and logistical constraints. In the near term, low cost approaches can be employed that at least help establish comparative baselines of new accretion by coral reef ecosystems. A number of techniques to measure net community calcification have been reported in the literature (Smith, S. V. and Key, G. S. 1975; Gattuso et al., 1999) and efforts are underway to refine modifications of these techniques for CRCP monitoring activities.

In addition, a key indicator of change in response to OA may be a reduction in the recruitment and viability of some forms of calcareous algae (CCA). Efforts are currently underway to evaluate the influence of local ambient carbonate chemistry on CCA abundance and accretion rates. In this approach, accretion plates are distributed along spatial gradients in carbonate chemistry to provide information on the relative rates of new accretion. The deployment, recovery, processing, and analysis of these accretion plates could be replicated at intermittent intervals to monitor changes over time to evaluate if trends may evolve that mimic expectations based upon laboratory results indicating a strong OA impact on CCA.

Furthermore, there are many sources of calcium carbonate production that contribute to coral reef building. Some calcium carbonate production contributes to the coral reef framework (e.g., reef-building corals), some to coral reef sediments (e.g., detrital skeletal material and CCA (*Halimeda*)), and some to binding coral reef materials (e.g., encrusting coralline algae and marine cements). Early marine cementation is thought to be a key factor that promotes rigidity and stability of coral reef framework materials. Little is known about the influence of OA on coral reef cementation and whether changes in cementation rates will impact coral reef resistance to erosion. Quantification of cement abundance and mineralogy could offer an additional ecological indicator which should be evaluated and tracked over time. Indeed, recent studies (Manzello et al., 2008) that coral reefs in the Eastern Tropical Pacific (ETP) where modern day carbonate chemistry is analogous to future conditions exhibit anomalously low cement abundance.



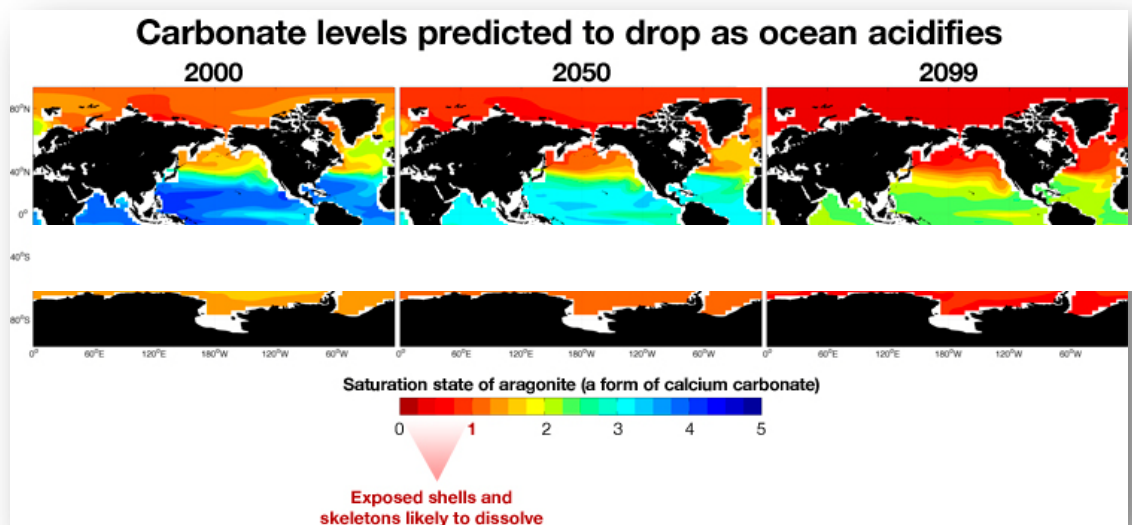
*Figure 6. Eastern Tropical Pacific reefs represent a real world example of coral reef growth in low saturation state waters that provide insights into how the biological-geological interface of coral reef ecosystems will change in a high carbon dioxide world (Manzello et al., 2008).*

#### *Research Priorities Locations:*

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When considering the placement of long-term diagnostic monitoring for OA, it is important to consider the geographic distribution of surface carbonate chemistry. In general, higher latitudes exhibit lower aragonite saturation states, but greater seasonality primarily due to changes in temperatures. Surface waters tend to be increasingly supersaturated with respect to carbonate mineral phases closer to the equator. In fact, carbonate mineral saturation state has been cited as a first-order determinant governing the distribution of prominent coral reef ecosystems in latitudes less than 30 degrees (Kleypas et al., 1999). As OA progresses over the next century the latitudinal extent of coral reef ecosystems is expected to contract towards the equator. Based upon this global distribution pattern, monitoring strategies should be distributed broadly along latitudinal transects in both the Atlantic/Caribbean and Pacific Ocean basins. However, while nearly all high latitude coral reef ecosystems exhibit relatively low carbonate mineral saturation states, this does not necessarily imply the inverse is true for low





*Figure 7. A model depicting the distribution of aragonite saturation state in the surface oceans and the projected changes during this century under business as usual emission scenarios and readapted for Oceanus (Feely et al., 2009).*

latitude systems. In the Pacific, as a consequence of equatorial upwelling, locations like Jarvis Island can experience quite low values as well. Thus, care must be given to establishing latitudinal transects in each basin to maximize observations over chemical gradients.

Another important consideration is the amount of coastal influence a site receives. Monitoring sites need to track changes in chemistry on the order of only 3% per decade. This becomes increasingly difficult to resolve in ecosystems where coastal biogeochemical processes can induce significant short-term and complex variability. Many of the remote Pacific Islands exhibit limited coastal interference (e.g., Kingman Atoll is nearly completely submerged) which can be advantageous when seeking to track changes explicitly attributed to global environmental change. Such ecosystems are far less available in the Atlantic/Caribbean region with perhaps the notable exception of the Flower Garden Banks in the Gulf of Mexico.

#### *Expected Outcomes:*

The outcomes of these efforts will provide a diagnostic monitoring capability for the rate and magnitude of OA in coral reef ecosystems, as well as the ecological response to those changes. As an increasing number of studies demonstrate potentially significant consequences for coral reef ecosystems structure and function in response to OA, it is imperative that *in situ* monitoring efforts are designed to test the laboratory based assumptions.

**Description of the Problem:**

The most significant impacts of OA to marine ecosystems will likely transpire over the next several decades as the rates and magnitude of chemical changes continue to accelerate relative to pre-industrial levels. Thus far, surface ocean pH has declined by about 0.1 units since the pre-industrial period as a consequence of OA. However, estimates based on the Intergovernmental Panel on Climate Change business as usual emission scenarios suggest that atmospheric carbon dioxide levels could approach 800 parts per million near the end of the century corresponding to a surface water pH change of 0.3 pH units. This change will represent an increase in the ocean's acidity of about 150% (Feely et al., 2009). Such projections in the open ocean are reasonably certain. However in shallow water coral reef ecosystems where local processes can dominate, such projections become more uncertain.

Improving modeling capabilities to better capture the complexity of coral reef ecosystems will allow for evaluating whether areas are more or less resilient to the impacts of OA and serve as the primary tool to inform management with intervention and adaption strategies. The development of these model projections will need to anticipate not only the rates and magnitude of change in near coral reef carbonate chemistry, but will need to also predict the ecosystem response in terms of the impacts to structure, function and biodiversity. This will require the development and integration of climate, carbon, and ecological models informed by manipulative experiments and targeted field process studies.

**Task 3.1: What are the chemical consequences of continued ocean acidification in near coral reef waters under different atmospheric carbon dioxide concentrations and are there important geochemical thresholds which could be exceeded?**

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**Approach: Investigate coral reef ecosystems currently exposed to analogous future conditions and develop geochemical models to yield more accurate projections of ocean acidification in coral reef ecosystems.**

In order to better discern when OA thresholds might be crossed in future decades, it will be important to advance the development of coupled climate and carbon cycling models that assimilate the observations and findings of the process investigations and monitoring under the preceding tasks. The models will need to account for the local biogeochemical processes that could alter the rates of OA and serve as a prerequisite for developing realistic ecological response projections to OA. Currently, most models adopt a simplified assumption that carbonate chemistry at coral reefs equates to the neighboring oceanic waters. However, this is now known to be a false assumption under most cases and new models are needed to focus on resolving the local complexity in the carbonate chemistry in coral reef ecosystems.

### **Task 3.2: How will coral reef ecosystems respond to ocean acidification in the future and which ecosystems might prove most resilient?**

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**Approach: Conduct ocean acidification manipulative laboratory and field experiments to develop improved coral ecosystem models.**

Controlled exposure laboratory experiments and comparative field studies that examine coral reef ecosystem response across natural carbonate chemistry are needed. These experiments will need to consider the interactions between the effects of OA and other variables such as temperature, nutrients, light, and trace metals, as well as the impacts of realistic changes in reduced carbonate saturation states on all life stages including survival, growth, reproduction and development. The studies should be conducted across a variety of vulnerable organisms with particular emphasis placed on those species that are ecologically or economically important. Processes currently known to be affected by OA (e.g., calcification, dissolution and nitrogen fixation) are ripe for investigation at the ecosystem level, either in mesocosms or in small scale field experiments, and should be the focus for near-term research.

Additionally, genomic approaches should be coordinated with experiments as appropriate to provide insights into the mechanisms that show organism resilience to OA changes. Global gene expression profiling with microarrays has been successfully used to explore the effects of OA on the physiology and distribution of calcifying marine organisms (Hofmann et al., 2008; O'Donnell et al., 2009) and is rapidly becoming an established tool in marine ecology (Dupont et al., 2008).

### **Task 3.3: What are the cumulative impacts of multiple stressors acting in conjunction or synergistically with ocean acidification?**

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**Approach: Develop cumulative impact models that account for the effects of ocean acidification.**

OA does not occur in isolation and it is important to understand its effects on thermal stress, sea-level rise, stratification and nutrient availability, and storm intensity in a changing climate. The resulting cumulative effects are likely non-linear and the non-equilibrium state of marine ecosystems can limit the applicability of simple empirical and statistical based predictions. Cumulative impact models are needed to incorporate the effects of OA with the most up to date scientific information. However, empirical models are limited (Silverman et al., 2009, Kleypas et al., 1999) and not readily tailored to meet regional management needs. A key recommendation from the joint agency St. Petersburg report (Kleypas et al., 2006) was to conduct a census of existing ecological models that can be adapted to incorporate carbon cycle modeling. There is a need to identify and adapt ecological models that incorporate the observational and experimental outputs of the preceding research and monitoring activities described in this plan.



### *Research Priorities Locations:*

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A number of natural laboratories exist whereby existing carbonate chemistry more or less mimics conditions anticipated over this century and beyond. This includes areas where natural upwelling drives carbon dioxide enriched waters to the surface causing them to exhibit rather low pH and carbonate mineral saturation states. As previously mentioned, the ETP is one such location where considerable research has been conducted and could be further extended. The westernmost edge of Jarvis Island also experiences similarly low carbonate mineral saturation states perhaps intermittently with El Niño/La Niña Southern Oscillation cycles which drive upwelling. Other natural laboratories include locations where marine volcanic carbon dioxide vents can alter local ocean chemistry (Hall-Spencer et al., 2008).

A number of NOAA laboratories and science centers (e.g., Alaska Fisheries Science Center, Northwest Fisheries Science Center, and Northeast Fisheries Science Center) are currently equipped and actively engaged in conducting carbon dioxide manipulation experiments on a range of organisms at different life stages. While most of these experiments involve shellfish, finfish and planktonic species, the facilities and expertise could be adapted to accommodate coral reef related species. Furthermore, NOAA (e.g., AOML and the Southeast Fisheries Science Center) together with academic partners have historically been engaged in similar efforts specific to coral reef organisms.

Cumulative impact model development is likely best advanced through external research grants and/or directed studies through NOAA's Cooperative Institutes.

### *Expected Outcome:*

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The outcome of these efforts will provide ecological forecast capabilities at the jurisdictional and regional level. The ecological forecast will provide an important decision support tool to inform policy discussions on the specific consequences of different carbon emission scenarios. It will also provide insights into discerning specific areas which might serve as refugia from OA impacts and therefore could be used to guide coral reef management.

### Description of the Problem:

As OA impacts to coral reef ecosystems are better understood, it will be important to deliver pertinent information and decision support tools to managers so that they can better understand the vulnerability of their managed ecosystems and develop appropriate management actions. Currently, the only strategy for coping with the additional stress of climate change and OA is to increase overall coral reef resilience. Traditionally protected areas, especially those established in the past, have been designed without taking resilience principles under consideration. As was recently observed (Graham et al., 2008), in the case of no-take areas, the effects of climate scale processes on coral reef ecosystems appear spatially variable at multiple scales, with impacts and vulnerability affected by geography, but not management regime. While existing no-take marine protected areas still support high biomass of fish, these areas have no positive effect on the ecosystem response to large scale disturbances such as climate change. It was not the purpose for which they were designed. Graham suggests “a need for future conservation and management efforts to identify and protect regional refugia integrated into existing management frameworks and combined with policies to improve system wide resilience to climate variation and change”. Before an area of refugia can be identified and protected, what constitutes an area of refugia in terms of OA (e.g., chemical and community setting) must first be defined based on the preceding research and monitoring efforts.

### Task 4.1: What local management actions will foster the greatest resilience to ocean acidification?

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#### Approach: Identify strategies to foster local carbon uptake with coral reef ecosystems.

The near coral reef carbonate chemistry is a reflection not only of the prevailing ocean state, but also the net influence of a number of physical and biological processes including mineral precipitation and dissolution, photosynthesis, respiration, and calcification. Generally, the ratio of photosynthesis to respiration is about one to one within a coral reef, whereby the carbon dioxide added to the surrounding coral reef waters by respiration at night tends to be balanced by that taken up due to photosynthesis during the day. However, this simple balance can be compromised by the addition of local organic carbon sources and nutrients (e.g., coastal run-off) which can result in elevated levels of carbon dioxide and hence depressed aragonite saturation state by enhancing respiration over photosynthesis. While our knowledge of the carbon budget and cycling among coral reefs is still limited, it is apparent that there are differences in the mode of carbon cycling among coral reefs (Suzuki and Kawahata, 1999 and 2003). A system level net organic to inorganic carbon production ratio is a master parameter for controlling how much a coral reef ecosystem serves to alter its ambient chemical environment. The extent to which local management actions can maintain a well balanced productivity to respiration rate through fostering healthy associated seagrass beds and limiting

local pollution inputs should be an area for intense investigation to develop local mitigation strategies.

#### **Task 4.2: How can ocean acidification be incorporated into fishery models?**

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**Approach: Develop ecosystem based fishery models that account for the impact of ocean acidification.**

Given the complexity of the challenges resource managers' face, effective management is based on the proper understanding of coral reefs as ecosystems and of the complex and often synergistic impacts of different stressors, including OA. Ecosystem based fisheries models represent a potentially powerful decision support tool that can visualize outcomes of ecosystem impacts of various OA scenarios on fish communities and production under any given management strategy (Holmes and Johnstone, 2010; Melbourne-Thomas et al., 2011). Efforts are needed to develop models that incorporate the observational and experimental outputs of the preceding research and monitoring activities. These models can then be provided to regional and local managers to inform management action.

An example of such an ecosystem based fisheries modeling framework that accounts for OA and other stressors to corals and coral reef ecosystems is the Atlantis Ecosystem Model (Fulton, 2001) for temperate marine ecosystems. Atlantis is an ecosystem box model (Fulton et al., 2004a) intended for use in management strategy evaluation (De la Mare, 1996; Sainsbury et al., 2000) and has been applied to multiple marine ecosystems in Australia and the U.S. to identify food web interactions with OA impacts. The model tracks the nutrient flows through the main biological groups found in the marine ecosystem of interest with a fisheries and management submodel simulating monitoring and assessment.

#### **Task 4.3: What tools are available to assist managers in applying the best available science to inform management action?**

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**Approach: Contribute to the development of tools and a climate change adaption guide for resource managers.**

Guidelines for incorporating OA into fisheries and coastal resource management and methodologies for climate change and OA vulnerability assessments for coastal and marine natural resources are needed. The development of *Adapting to Climate Change: A Guide for Coral Reef Managers* is planned to expand on *A Reef Manager's Guide to Coral Bleaching* (Marshall and Schuttenberg, 2006) through a long-term partnership with the Great Barrier Reef Marine Park Authority, the International Union for Conservation of Nature and others. The intent is to incorporate these guidelines and meet three critical needs of resource managers: increased knowledge of climate change, OA and associated risks for coral reefs; accessible and relevant resources to support vulnerability assessments and communication about climate change issues for coral reefs; and identification and explanation of strategies that can be

integrated into planning processes to enhance coral reef resilience and help coral reef dependent communities and industries adapt to climate change. While multiple recent efforts provide critical general and theoretical underpinnings for adaptation planning, a synthesis of more specific guidance for coral reefs is needed to support appropriate adaptation actions for these highly sensitive ecosystems. Coral reef managers need a systematic approach for connecting the theoretical to the practical given the specific management context and scales in which they work and the complexity of weighing and prioritizing among sometimes conflicting management actions.

#### *Research Priorities Locations:*

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Jurisdictions where nutrient loading and coastal runoff are identified as important drivers of the water chemistry and where local management actions can facilitate change will be priority areas. Ecosystem based fishery models are needed in all U.S. jurisdictions and local resource managers and priority international geographies should have access to decision support tools based on the best available OA science.

#### *Expected Outcomes:*

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Ultimately while the primary control on OA impacts lies with international policy decisions governing net carbon emissions, an informed resource management community will be better prepared to adapt to changes and in some instances may help to delay the onset of OA impacts. Resource managers receive tools based on the best available science to incorporate ecological forecasts and develop guidelines for management activities.

### **Engagement and Outreach**

OA is an emerging environmental topic that is generating increased interest amongst a growing section of the public (e.g., students, educators and policy makers). It is also a topic that is not easily grasped by a lay audience. As an emerging topic, there are relatively few complete and innovative resources for the public to understand OA, especially when compared to educational products for other long established environmental issues. NOAA and partners are uniquely positioned to take a lead role in guiding the development of OA educational and communication products that are scientifically accurate, and utilize the best education and communication practices to familiarize the public with this issue, capacitate educators to teach OA effectively in the classroom and support student engagement in the topic. To understand the CRCP's approach for coral reef ecosystems, please refer to the *CRCP National Communication, Education and Outreach Strategy*. The strategy provides overarching guidance to better focus, integrate, and synchronize activities in formal and informal education programs, strategic communication activities, social marketing campaigns and outreach activities.

## References

- Albright R., B. Mason, and C. Langdon. 2008. Effect of aragonite saturation state on settlement and post-settlement growth of *Porites astreoides* larvae. *Coral Reefs*, Vol. 27, no. 3, pp. 485-490.
- Albright, R. A., B. Mason, M. Miller, and C. Langdon. 2010. Ocean acidification compromises recruitment success of the threatened Caribbean coral, *Acropora palmata*. *Proceedings of the National Academy of Sciences* 107:20400-20404.
- Amaral-Zettler, L., J. E. Duffy, et al. 2011. Attaining an operational marine biodiversity observation network (BON): Synthesis report. National Oceanographic Partnership Program, White Paper: 28 pp.
- Anthony, K. R. N., D. I. Kline, et al. 2008. "Ocean acidification causes bleaching and productivity loss in coral reefs builders." *PNAS*, 105(45): 17442-17446.
- Anthony, K. R. N., J. A. Kleypas, and J.-P. Gattuso. 2011. Coral reefs modify their seawater carbon chemistry - implications for impacts of ocean acidification, *Global Change Biology*, 17(12), 3655-3666.
- Bak, R. P. M., G. Nieuwland, and E. H. Meesters. 2009. Coral growth rates revisited after 31 years: What is causing lower extension rates in *Acropora palmata*? *Bulletin of Marine Science* 84:287-294.
- Bates, N.R. 2007. Interannual variability of the oceanic CO<sub>2</sub> sink in the subtropical gyre of the North Atlantic Ocean over the last two decades. *J. Geophys. Res.* 112 C09013, doi:10.1029/2006JC003759.
- Balch, W.M., and P.E. Utgoff. 2009: Potential interactions among ocean acidification, coccolithophores, and the optical properties of seawater. *Oceanography*, 22, 146–159.
- Balch, W.M., and P.E. Utgoff. 2009: Potential interactions among ocean acidification, coccolithophores, and the optical properties of seawater. *Oceanography*, 22, 146–159.
- Borowitzka, M. A. 1981. Photosynthesis and calcification in the articulated coralline alga *Amphiroa anceps* and *A. foliaceae*, *Mar. Biol.* 62, 17 – 23.
- Brown, C. J., E. A. Fulton, A. J. Hobday, R. J. Matear, H. P. Possingham, C. Bulman, V. Christensen, R. E. Forrest, P. C. Gehrke, N. A. Gribble, S. P. Griffiths, H. Lozano-Montes, J. M. Martin, S. Metcalf, T. A. Okey, R. Watson, and A. J. Richardson. 2010. Effects of climate-driven primary production change on marine food webs: implications for fisheries and conservation. *Global Change Biology* 16:1194-1212.
- Cantin NE, Cohen AL, Karnauskas KB, Tarrant AM, McCorkle DC. 2010. Ocean warming slows coral growth in the central Red Sea. *Science* 329:322-325
- Cesar, H, Burke, L and Pet-Soede, L. 2003. The economics of worldwide coral reef degradation, Cesar Environmental Economics Consulting: Arnhem (Netherlands), 23 pp.
- Cheung et al. 2009. Protecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*. 10: 235-251.

Cohen AL, McCorkle DC, de Putron S, Gaetani GA, Rose KA. 2009. Morphological and compositional changes in the skeletons of new coral recruits reared in acidified seawater: Insights into the biomineralization response to ocean acidification. *Geochem Geophys Geosys* 10:Q07005.

Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. 2007. Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.) Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Cohen, A., M. Holcomb. 2009. Why Corals Care About Ocean Acidification: Uncovering the Mechanism. *Oceanography*. Vol. 22, no. 4, p. 118.

Cooper, T.F., G. De'ath, K.E. Fabricius, J.M. Lough. 2008. Declining coral calcification in massive Porites in two nearshore regions of the northern Great Barrier Reef. *Glob. Change Biol.* 14, 529.

De'ath, G., J.M. Lough, and K.E. Fabricius. 2009. Declining coral calcification on the Great Barrier Reef. *Science* 323:116-119.

Edmunds, P.J. 2007. Evidence for a decadal-scale decline in the growth rates of juvenile scleractinian corals. *Mar. Ecol. Prog. Ser.* Vol. 341, pp. 1-13.

De la Mare, W.K. 1996. Some recent developments in the management of marine living resources. In *Frontiers of Population Ecology*, pp. 599–616. Ed. by R. B. Floyd, A. W. Shepherd, and P. J. De Barro. CSIRO Publishing, Melbourne, Australia.

DOE, 1994. Handbook of methods for the analysis of the various parameters of the carbon dioxide system in seawater. In: Dickson A. G. & Goyet C. (Eds.), *Carbon Dioxide Information Analysis Center*, Oak Ridge National Laboratory.

Dupont, S., J. Havenhand, W. Thorndyke, L. Peck, and M. Thorndyke. 2008. Near-future level of CO<sub>2</sub> driven ocean acidification radically affects larval survival and development in the brittlestar *Ophiothrix fragilis*. *Marine Ecology-Progress Series* 373:285-294.

Fabry, V.J. et al. 2008. Present and future impacts of ocean acidification on marine ecosystems and biogeochemical cycles, Report of the Ocean Carbon and Biogeochemistry Scoping Workshop on Ocean Acidification Research, La Jolla, California.

Feely, R.A., C.L. Sabine, J.M. Hernandez-Ayon, D. Ianson, and B. Hales. 2008. Evidence for upwelling of corrosive "acidified" water onto the continental shelf. *Science*, 320, 1490–1492.

Feely, R.A., S.C. Doney, and S. Cooley. 2009. Ocean acidification: present conditions and future changes in a high- CO<sub>2</sub> World. *Oceanography*, 22, 36–47.

Fulton, E. A. 2001. The effects of model structure and complexity on the behaviour and performance of marine ecosystem models. University of Tasmania, Hobart.

Fulton, E.A., M. Fuller, A.D.M. Smith, and A.E. Punt. 2004a. Ecological Indicators of the Ecosystem Effects of Fishing: Final Report. Australian Fisheries Management Authority Report, R99/1546.

Fulton, E. A., A. D. M. Smith, and C. R. Johnson. 2004b. Effects of spatial resolution on the performance and interpretation of marine ecosystem models. *Ecological Modelling* 176:27-42.

Gao, K., Y. Aruga, K. Asada, T. Ishihara, T. Akano, and M. Kiyohara. 1993. Calcification in the articulated coralline alga *Corallina pilulifera*, with special reference to the effect of elevated CO<sub>2</sub> concentration, *Mar. Biol.*, 117, 129-132.

Gattuso, Jean-Pierre; Payri, Claude E; Pichon, Michel; Delesalle, Bruno; Frankignoulle, Michel. 1997. Primary production, calcification, and air-sea CO<sub>2</sub> fluxes of a macroalgal-dominated coral reef community (Moorea, French Polynesia). *Journal of Phycology*, 33(5), 729-738, doi:10.1111/j.0022-3646.1997.00729.x

Gattuso J. P., M. Frankignoulle, I. Bourge, S. Romaine, and R. W. Buddemeier. 1998. Effect of calcium carbonate saturation of seawater on coral calcification, *Global and Planetary Change*, 18, 37.

Gattuso J-P, Frankignoulle M, Smith SV. 1999. Measurement of community metabolism and significance in the coral reef CO<sub>2</sub> source-sink debate. *Proceedings of the National Academy of Sciences* 96:13017-22.

Ginsburg, R. N. 1983. Geological and biological roles of cavities in coral reefs. Perspectives on coral reefs. D. J. Barnes. Townsville, Australian Institute of Marine Science: 148-153.

Gledhill, D. K., R. Wanninkhof, et al. 2008. Ocean acidification of the Greater Caribbean Region 1996–2006. *Journal of Geophysical Research* 113(C10).

Gledhill, D, R. Wanninkhof, and M. Eakin. 2010. Observing ocean acidification from space, *Oceanography* 22(4): 48-59.

Glynn PW. 1997. Bioerosion and coral reef growth: a dynamic balance. *Life and Death on Coral Reefs*, ed Birkeland C (Chapman and Hall, New York), pp 68–95.

Graham NAJ, McClanahan TR, MacNeil MA, Wilson SK, Polunin NVC, et al. 2008. Climate Warming, Marine Protected Areas and the Ocean-Scale Integrity of Coral Reef Ecosystems. *PLoS ONE* 3(8): e3039. doi:10.1371/journal.pone.0003039.

Gratwicke, B. and M.R. Spieght. 2005. Effects of habitat complexity on Caribbean marine fish assemblages. *Mar. Ecol. Prog. Ser.* Vol. 292, pp. 301-310.

Hall-Spencer, J.M., et al. 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature*. 454(3):96-99.

Helmle, K. P., and R. E. Dodge. 2011. Sclerochronology, in *Encyclopedia of Modern Coral Reefs; Structure, Form and Process*, edited by D. Hopley, pp. 958-966, Springer Verlag. Doi:10.1007/978-90-481-2639-2\_22

Helmle, K. P., R. E. Dodge, P. K. Swart, D. K. Gledhill, and C. M. Eakin. 2011. Growth rates of Florida corals from 1937 to 1996 and their response to climate change. *Nature Communications*. 2:215 doi: 10.1038/ncomms1222.

- Hendriks, I.E., C.M. Duarte, M. M. A'lvarez. 2010. Vulnerability of marine biodiversity to ocean acidification: A meta-analysis. *Estuarine, Coastal and Shelf Science*, 86, pp 157-164  
doi:10.1016/j.ecss.2010.06.007
- Hofmann, G. E., M. J. O'Donnell, and A. E. Todgham. 2008. Using functional genomics to explore the effects of ocean acidification on calcifying marine organisms. *Marine Ecology-Progress Series* 373:219-225.
- Holcomb M, McCorkle DC, Cohen AL. 2010. Long-term effects of nutrient and CO<sub>2</sub> enrichment on the temperate coral *Astrangia*. *J Exp Mar Biol Ecol* 386:27–33.
- Holmes, G. and R. W. Johnstone. 2010. Modelling coral reef ecosystems with limited observational data. *Ecological Modelling* 221:1173-1183.
- Ives. A.R. et al. 2007. Stability and diversity of ecosystems. *Science* 317:58-62.
- Jury CP, Whitehead RF, Szmant AM. 2009. Effects of variations in carbonate chemistry on the calcification rates of *Madracis auretenra* (= *Madracis mirabilis* sensu Wells, 1973): bicarbonate concentrations best predict calcification rates. *Global Change Biol* 16:1632–1644.
- Kleypas, J.A., R.W. Buddemeier, D. Archer, J.P.Gattuso, C. Langdon, and B.N. Opdyke. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science*, 284, 118–120.
- Kleypas, J.A. et al. 2006. Impacts of Increasing Ocean Acidification on Coral Reefs and Other Marine Calcifiers: A Guide for Future Research, report of a workshop held 18–20 April 2005, St. Petersburg, FL, sponsored by NSF, NOAA, and the U.S. Geological Survey, 90 pp.
- Keul, N., Morse, J. M., Wanninkhof, R., Gledhill, D. K., & Bianchi, T. S. 2010. Carbonate Chemistry Dynamics of Surface Waters in the Northern Gulf of Mexico. *Aquatic Geochemistry* 16(3):1573-1421.
- Knowlton, N, RE Brainard, MJ Caley, R Fisher, M Moews, L Plaisance. 2010. Coral Reef Biodiversity. In: *Life in the world's oceans: diversity, distribution, and abundance*, Edited by AD McIntyre. Blackwell Publishing Ltd, pp. 65-78.
- Langdon C. and M. J. Atkinson. 2005. Effect of elevated pCO<sub>2</sub> on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment, *Journal of Geophysical Research*, 110(C09S07).
- Langdon C., T. Takahashi, C. Sweeney, D. Chipman, and J. Goddard. 2000. Effect of carbonate saturation state on the calcification rate of an experimental coral reef, *Global Biogeochem. Cycles*, 14(2), 639-654.
- Langdon, C., W. S. Broecker, D. E. Hammond, E. Glenn, K. Fitzsimmons, S. G. Nelson, T.-H. Peng, I. Hajdas, and G. Bonani. 2003. Effect of elevated CO<sub>2</sub> on the community metabolism of an experimental coral reef, *Global Biogeochem. Cycles*, 17, 1011, oi:10.1029/ 2002GB001941.
- Leclercq, N., J.-P. Gattuso, and J. Jaubert. 2000. CO<sub>2</sub> partial pressure controls the calcification rate of a coral community, *Global Change Biol.*, 6, 329-334.



- Leclercq, N., J.-P. Gattuso, and J. Jaubert. 2002. Primary production, respiration, and calcification of a coral reef mesocosm under increased CO<sub>2</sub> partial pressure, *Limnol. Oceanogr.*, 47, 558-564.
- Lough, J.M. 2008. Coral calcification from skeletal records revisited. *Mar. Ecol. Prog. Ser.* Vol. 373, pp. 257-264. 2008.
- Lugo-Fernandez, A., H.H. Roberts, J.N. Suhayda. 1998. Wave transformations across a Caribbean fringing-barrier coral reef. *Cont. Shelf Res.* Vol. 18, no. 10, pp. 1099-1124.
- Manzello, D. P., J. A. Kleypas, et al. 2008. "Poorly cemented coral reefs of the eastern tropical Pacific: Possible insights into reef development in a high-CO<sub>2</sub> world." *Proceedings of the National Academy of Sciences of the United States of America* 105(30): 10450-10455.
- Manzello DP. 2009. Reef development and resilience to acute (El Niño warming) and chronic (high-CO<sub>2</sub>) disturbances in the eastern tropical Pacific: a real-world climate change model. *Proc. 11th Intl Coral Reef Symposium*, 1299-1304.
- Manzello, D. P. 2010. Ocean acidification hotspots: spatiotemporal dynamics of the seawater CO<sub>2</sub> system of eastern Pacific reefs. *Limnol Oceanogr* 55, 239-248.
- Macintyre, I. G., K. Rutzler, J.N. Norris, and K. Fauchald. 1982. A submarine cave near Columbus Cay, Belize: a bizarre cryptic habitat. *Smithsonian Contributions to the Marine Sciences*: 127-141.
- Marshall, A. T., and P. Clode. 2002. Effect of increased calcium concentration in sea water on calcification and photosynthesis in the scleractinian coral *Galaxea fascicularis*, *J. Exp. Biol.*, 205, 2107–2113.
- Marshall, P. A., and H. Z. Shuttenberg. 2006. *A Reef Manager's Guide to Coral Bleaching*. Great Barrier Reef Marine Park Authority, Townsville, QLD, Australia.
- Marubini, F., H. Barnett, C. Langdon, and M. J. Atkinson. 2001. Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*, *Mar. Ecol. Prog. Ser.*, 220, 153-162.
- Marubini, F., C. Ferrier-Pages, and J.-P. Cuif. 2002. Suppression of growth in scleractinian corals by decreasing ambient carbonate ion concentration: A cross-family comparison, *Proc. R. Soc. London, Ser. B*, 270, 179-184.
- Melbourne-Thomas, J., C. R. Johnson, P. M. Aliño, R. C. Geronimo, C. L. Villanoy, and G. G. Gurney. 2011. A multi-scale biophysical model to inform regional management of coral reefs in the western Philippines and South China Sea. *Environmental Modelling & Software* 26:66-82.
- Morita M, et al. 2010. Ocean acidification reduces sperm flagellar motility in broadcast spawning reef invertebrates. *Zygote* 18:103–107.

- Morse, J. W., Andersson, A. J., and Mackenzie, F. T. 2006. Initial responses of carbonate-rich shelf sediments to rising atmospheric pCO<sub>2</sub> and ocean acidification: role of high Mg-calcites, *Geochim. Cosmochim. Acta*, 70, 5814–5830, 2006.
- Munday PL, Dixson DL, Donelson DL, Jones GP, Pratchett MS, Devitsina G, Doving KB. 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *PNAS* 106:1848-1852
- Munday P. L., Gagliano M., Donelson J. M., Dixson D. L., & Thorrold S. R. 2011. Ocean acidification does not affect the early life history development of a tropical marine fish. *Marine Ecology Progress Series* 423:211-221.
- O'Donnell, M., L. Hammond, and G. Hofmann. 2009. Predicted impact of ocean acidification on a marine invertebrate: elevated CO<sub>2</sub> alters response to thermal stress in sea urchin larvae. *Marine Biology* 156:439-446.
- Ohde, S., and M. M. Hossain. 2004. Effect of CaCO<sub>3</sub> (aragonite) saturation state of seawater on calcification of *Porites* coral, *Geochem. J.*, 38, 613-621.
- Orr J. C., V. J. Fabry, O. Aumont, L. Bopp, S. C. Doney, R. A. Feely, A. Gnanadesikan, N. Gruber, A. Ishida, F. Joos, R. M. Key, K. Lindsay, E. Maier-Reimer, R. Matear, P. Monfray, A. Mouchet, R. G. Najjar, G.-K. Plattner, K. B. Rodgers, C. L. Sabine, J. L. Sarmiento, R. Schlitzer, R. D. Slater, I. J. Totterdell, M.-F. Weirig, Y. Yamanaka, and A. Yool. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms, *Nature*, 437, 681.
- Pearson, P. N. and M. R. Palmer. 2000. Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature* 406(6797): 695-699.
- Raupach MR et al. 2007. Global and regional drivers of accelerating CO<sub>2</sub> emissions. *Proceedings of the National Academy of Sciences* 14: 10288-10293. <http://www.pnas.org/content/104/24/10288>.
- Reynaud, S., N. Leclercq, S. Romaine-Lioud, C. Ferrier-Pages, J. Jaubert, and J.-P. Gattuso. 2003. Interacting effects of CO<sub>2</sub> partial pressure and temperature on photosynthesis and calcification in a scleractinian coral, *Global Change Biol.*, 9, 1660– 1668.
- Riebesell, U. 2008. Acid test for marine biodiversity. *Nature*. 454(3): 46-47.
- Riebesell U., Fabry V. J., Hansson L. & Gattuso J.-P. (Eds.). 2010. Guide to best practices for ocean acidification research and data reporting, 260 p. Luxembourg: Publications Office of the European Union.
- Ries JB, Cohen AL, McCorkle DC. 2009. Marine calcifiers exhibit mixed responses to CO<sub>2</sub>-induced ocean acidification. *Geology* 37:1131–1134.
- Ries, J.B., A.L. Cohen, D.C. McCorkle. 2010. A nonlinear calcification response to CO<sub>2</sub>-induced ocean acidification by the coral *Oculina arbuscula*. *Coral Reefs*. 29:661–674.

Rodolfo-Metalpa R, Martin S, Ferrier-Pages C, Gattuso JP. 2010. Response of the temperate coral *Cladocora caespitosa* to mid and long-term exposure to pCO<sub>2</sub> and temperature levels projected for the year 2100 AD. *Biogeosci* 7:289–300.

Saenger, C., A. L. Cohen, D. W. Oppo, R. B. Halley, J. E. Carilli. 2009. Surface temperature trends and variability in the low-latitude North Atlantic since 1552, *Nature Geosciences*, 1-4, doi:10.1038/NGEO552.

Sala E., and N. Knowlton. 2006. Global marine biodiversity trends. *Annual Review Environment and Resources*, 31: 93-122.

Sainsbury, K.J., A.E. Punt A.E. and A.D.M. Smith. 2000. Design of operational management strategies for achieving fishery ecosystem objectives. *ICES Journal of Marine Science*, 57: 731–741.

Salisbury, J., M. Green, C. Hunt, and J. Campbell. 2008. Coastal acidification by rivers: A threat to shellfish? *Eos Trans. AGU*, 89, 513–528.

Selkoe, K.A., B.S. Halpern, C.M. Ebert, E.C. Franklin, E.R. Selig, K.S. Casey, J. Bruno, R.J. Toonen. 2008. A map of human impacts to a “pristine” coral reef ecosystem, the Papaha<sup>o</sup>naumokua<sup>o</sup>kea Marine National Monument. *Coral Reefs*, 28:635–650.

Silverman, J., B. Lazar, L. Cao, K. Caldeira, and J. Erez. (2009) Coral reefs may start dissolving when atmospheric CO<sub>2</sub> doubles. *Geophys. Res. Lett.* 2009. DOI: 10.1029/2008GL036282.

Small A., A. Adey, and D. Spoon. 1998. Are current estimates of coral reef biodiversity too low? The view through the window of a microcosm. *Atoll Research Bulletin*, 458: 1-20.

Smith, S.V. and Key, G.S. 1975. Carbon dioxide and metabolism in marine environments. *Limnology and Oceanography* 20:493-495.

Suwa, R., Nakamura, M., Morita, M., Shimada, K., Iguchi, A., Sakai, K., Suzuki, A. 2010. Effects of acidified seawater on early life stages of scleractinian corals (Genus *Acropora*). *Fisheries Science* 76, 93-99.

Suzuki, A. and H. Kawahata. 1999. Partial pressure of carbon dioxide in coral reef lagoon waters: comparative study of atolls and barrier reefs in the Indo-Pacific Oceans. *J. Oceanogr.*, 55, 731–745.

Suzuki, A. and H. Kawahata. 2003. Carbon budget of coral reef systems: an overview of observations in fringing reefs, barrier reefs and atolls in the Indo-pacific region. *Tellus*, 55B, 428–444.

Tanzil, J.T.I., B.E. Brown, A.W. Tudhope, and R.P. Dunne. 2009. Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between 1984 and 2005. *Coral Reefs*, 28(2), pp 519-528.

Veron JEN, Hoegh-Guldberg O, Lenton TM, Lough JM, Obura DO, Pearce-Kelly R, Sheppard CRC, Spalding M, Stafford-Smith MG, Rogers AD. 2009. The coral reef crisis: The critical importance of < 350 ppm CO<sub>2</sub>. *Mar Poll Bull* 58:1428-1436.

Wilkinson, C. 2000. Status of coral reefs of the world: 2000. Australian Institute of Marine Science: Townsville, Australia.

Willis, K.J., M.B. Araujo, K.D. Bennet, B. Figueroa-Rangel, C.A. Froyd, and N. Myers. 2007. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362:175-186.

Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. C. Jackson, H. K. Lotze, F. Micheli, S. R. Palumbi, E. Sala, K. A. Selkoe, J. J. Stachowicz, and R. Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787-790.

Yates K. K. and R. B. Halley. 2006.  $\text{CO}_3^{2-}$  concentration and  $\text{pCO}_2$  thresholds for calcification and dissolution on the Molokai reef flat, Hawaii, *Biogeosciences*, 3, 1 – 13.