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DRAFT

Recovery Plan

Elkhorn Coral *(Acropora palmata)* and Staghorn Coral *(A. cervicornis)*

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Staghorn Coral *(Acropora cervicornis)*

Elkhorn coral *(A. palmata)*

DRAFT

Recovery Plan for Elkhorn Coral *(Acropora palmata)* and Staghorn Coral *(A. cervicornis)*

Prepared by:

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PREFACE

Congress passed the Endangered Species Act of 1973 (16 USC 1531 et seq., amended 1978, 1982, 1986, 1988) (ESA) to protect species of plants and animals endangered or threatened with extinction. The National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NMFS) and the U.S. Fish and Wildlife Service (FWS) share responsibility for the administration of the ESA. NMFS is responsible for most marine and anadromous species including the elkhorn coral *(Acropora palmata)* and the staghorn coral *(A. cervicornis)*.

NMFS listed both the elkhorn coral and the staghorn coral as threatened on May 9, 2006. Section 4(f) of the ESA directs NMFS and FWS to develop and implement recovery plans for species under their jurisdiction, unless such a plan would not promote the species' conservation. NMFS determined that a recovery plan would promote conservation of elkhorn and staghorn corals and assembled the *Acropora* Recovery Team (ART) to develop this recovery plan. The ART included coral scientists and management experts from state, territorial, and federal government agencies and the non-governmental sector.

NMFS agrees with the ART that the success of the *Acropora* recovery plan will depend on cooperation from state, territorial, and federal agencies and a long-term commitment to implementing and enforcing its recommendations.

DISCLAIMER

Recovery plans delineate actions that the available information indicates are necessary for the conservation and survival of listed species. Plans are published by NMFS, sometimes prepared with the assistance of recovery teams, contractors, state agencies, and others. Objectives will be obtained and any necessary funds made available subject to budgetary and other constraints affecting the parties involved, as well as the need to address other priorities. Nothing in this plan should be construed as a commitment or requirement that any federal agency obligate or pay funds in contravention of the Anti-Deficiency Act, 31 U.S.C. 1341, or any other law or regulation. Recovery plans do not necessarily represent the views or the official positions or approval of any individuals or agencies involved in the plan formulation, other than NMFS. They represent the official position of NMFS only after they have been signed by the Assistant Administrator. Approved recovery plans are subject to modification as dictated by new information, changes in the status of species, and the completion of recovery actions. Please check for updates and revisions at the website below before using.

LITERATURE CITATION SHOULD READ AS FOLLOWS:

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ADDITIONAL COPIES MAY BE OBTAINED FROM:

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Recovery plans can be downloaded from NMFS' website:
http://www.nmfs.noaa.gov/pr/recovery/plans.htm

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DEDICATION

Brian Keller
A Tribute to a Friend and Colleague

Dr. Brian D. Keller, a sage scientist, patient mentor and committed conservationist, friend to many, and beloved husband to Fiona Wilmot, passed away on March 10, 2010. Brian touched countless lives with his science and his humanity over the course of an outstanding 40-year career in the Florida Keys and Caribbean.

Keller was active in programs that included monitoring reefs and fish life in the Florida Keys National Marine Sanctuaries marine protected areas, recovery of the threatened elkhorn and staghorn corals, invasive species, effects of pollution in the environment, and causes of harmful algal blooms. He authored numerous scientific publications and taught at several Universities and served on numerous committees, including much work on this Acropora Recovery Plan before his untimely death.

He received a B.S. in Biochemistry from Michigan State University in 1970, and earned his M.A. and Ph.D. in Ecology and Evolution from Johns Hopkins University in 1973 and 1976, respectively. He was trained as an evolutionary ecologist at John Hopkins University under the direction of Jeremy Jackson, where he researched the ecology and coexistence of sea urchins in Jamaican seagrass meadows in the 1970s. He did postdoctoral research on coral and alpheid shrimp with Nancy Knowlton in the early 1980s in Jamaica, Venezuela, and Panama. Brian was a Director and Research Fellow of Discovery Bay Marine Laboratory, Jamaica, from 1984-1986, and the Manager of the Smithsonian Tropical Research Institutes Oil Spill Project from 1987-1994 in Panama.

The monumental Panamanian oil spill study, published in Science in 1989, was a major factor in the closure of the Florida coast to oil exploration or extraction. Few studies exist detailing the impact of oil spills on tropical marine environments making this work highly influential then and now.

As the first Executive Director of the Ecological Society of America in Washington, DC, Brian was first and foremost an ecologist with a deep understanding of basic theory that guided his thinking throughout his career. His wisdom as a conservationist and manager, and the respect and high regard of his peers, stemmed directly from his ecological sophistication and as his exceptional maturity of judgment.

Brian joined NOAA in 2000 as science coordinator of the Florida Keys National Marine Sanctuary. During his time with the sanctuary program, he helped lay the foundation for management zones in the Florida Keys and led efforts to measure their effectiveness. He was the architect of the sanctuary's research and monitoring plans and contributed to a decade of success for sanctuary management of the Keys.

With Dr. Keller, the Nation's ocean science community lost a giant in the study, management and conservation of the marine ecosystems of the Florida Keys, Gulf of Mexico and Caribbean. In his role as science coordinator with the Office of National Marine Sanctuaries, Brian dedicated himself to finding innovative ways to understand marine ecology and to create new tools for conserving the ocean world

he loved. Brian used these tools every day to promote science for management, and used his experience and knowledge to mentor others.

His wisdom impacted management decisions locally, regionally, and worldwide. His influence can be seen in courses that are taught on MPA management and science, and the implementation of science-based programs especially in the Caribbean. He remained focused on the ecosystem and, in particular, what constituted a healthy ecosystem. He was wholly committed to developing strategies to restore those that were degraded both from natural and man-made causes. Brian introduced many to the principles of "connectivity" long before it was a common concept.

Brian was a rare combination of warmth and intelligence. We will miss his accessibility, his intellectual generosity and his unflappable, calm demeanor. These traits, combined with his ability to listen (and hear), and his FM classical station-announcer voice, made him a powerful communicator. Accomplished scientist, ocean advocate, and close friend, Brian's memory will live on in the hearts and scientific work of his friends and colleagues in the Florida Keys and beyond.

ABBREVIATION LIST

AGRRA	Atlantic and Gulf Rapid Reef Assessment
ART	*Acropora* Recovery Team
ATONs	Aids to Navigation
BMPs	Best Management Practices
BRT	Atlantic *Acropora* Biological Review Team
$CaCO_3$	Calcium Carbonate
CBD	Center for Biological Diversity
CCA	Crustose Coralline Algae
CDIAC	Carbon Dioxide Information Analysis Center
CITES	Convention on the International Trade in Endangered Species
CO_2	Carbon Dioxide
DOM	Dissolved Organic Matter
EEZ	Exclusive Economic Zone
ESA	U.S. Endangered Species Act
FGBNMS	Flower Garden Banks National Marine Sanctuary
FKNMS	Florida Keys National Marine Sanctuary
FWC	Florida Fish & Wildlife Conservation Commission
FWS	U.S. Fish & Wildlife Service
GIS	Geographic Information System
INRMP	Integrated Natural Resource Management Plan
IPCC	Intergovernmental Panel on Climate Change
LBSP	Land-Based Sources of Pollution
LNG	Liquid Natural Gas
MLW	Mean Low Water
N	Nitrogen
NASKW	Naval Air Station Key West
NM	Nautical Miles
NMFS	National Marine Fisheries Service
NOAA	National Oceanic & Atmospheric Administration
NPS	National Park Service
NWR	National Wildlife Refuge
OCSLA	Outer Continental Shelf Lands Act

P	Phosphorous
PCE	Primary Constituent Element
pCO_2	Partial Pressure of Carbon Dioxide
SCUBA	Self-contained Underwater Breathing Apparatus
SML	Surface Mucopolysaccharide Layer
USGS	United States Geological Survey
USVI	U.S. Virgin Islands
WBD	White Band Disease
WPx	White Pox

EXECUTIVE SUMMARY

Current Species Status: Elkhorn *(Acropora palmata)* and staghorn *(A. cervicornis)* corals were listed as threatened under the ESA on May 9, 2006 (NMFS 2006). Elkhorn and staghorn corals were once the most abundant and important species on Atlantic/Caribbean coral reefs in terms of building reef structure. Both elkhorn and staghorn corals underwent precipitous declines in abundance throughout their ranges in the 1970s and 1980s. Although quantitative data on former distribution and abundance of these species are scarce, in the few locations where quantitative data are available (e.g., Florida Keys, Dry Tortugas, Jamaica, and the U.S. Virgin Islands), declines in abundance are estimated at greater than 97 percent. The significant loss of population density in both coral species has resulted in a reduction of their ability to successfully reproduce, either sexually or asexually. Data suggest the decline in Atlantic/Caribbean elkhorn and staghorn coral abundances is primarily the result of disease. Although disease was the primary cause of initial decline, other threats such as elevated seawater temperatures and ocean acidification are credible and potentially significant impediments to recovery of these species. Therefore, this recovery plan not only addresses threats documented to have caused the decline of elkhorn and staghorn coral populations, but identifies and addresses factors that are likely to negatively impact the survivial and recovery of these species. Furthermore, no single or collective group of threats may impact all regions of these species' ranges equally. Multiple threats acting synergistically or cumulatively likely compound impediments to recovery among elkhorn and staghorn coral populations. The threats to these species that are impeding recovery are: disease, increasing temperature, depensatory population effects, loss of recruitment habitat, sedimentation, anthropogenic abrasion and breakage, predation, inadequacy of existing regulatory mechanisms, natural abrasion and breakage, ocean acidification, and nutrients and contaminants.

Recovery Strategy: The purpose of this recovery plan is to identify a strategy for rebuilding and assuring the long-term viability of elkhorn coral and staghorn coral populations in the wild, allowing ultimately for the species' removal from the federal list of endangered and threatened species. Elkhorn and staghorn coral populations should be large enough so that successfully reproducing individuals comprise numerous populations (including thickets) across the historical ranges of these species and should be large enough to protect their genetic diversity and maintain their ecosystem functions. Threats to these species and their habitat must be sufficiently abated to ensure a high probability of survival into the future. The proposed recovery approach serves to address the most pressing gaps in knowledge, addresses critical demographic factors required for recovery, and targets the reduction or elimination of threats so that the recovery objectives outlined in this plan have the greatest likelihood of being achieved. Because many of the important threats to the recovery of elkhorn and staghorn corals are not directly manageable, the recovery strategy pursues simultaneous actions to address critical demographic factors, the range of threats, and knowledge gaps. The gaps in knowledge must be addressed through basic experimental and genetic research along with monitoring to determine the current condition of elkhorn and staghorn corals. Climate models and experimental research indicate that recovery of elkhorn and staghorn corals will be impeded by increasing ocean temperatures and acidification resulting from global atmospheric CO_2 levels. Therefore, actions must be taken to address ocean warming and acidification impacts on these species. Simultaneously, local threat reductions, mitigation strategies, and *in* and *ex situ* conservation and restoration actions must be pursued. These include reducing chronic or localized mortality sources (predation, anthropogenic physical damage, acute sedimentation, nutrients, and contaminants) and acute stresses (LBSP, physical disturbance threats). Population enhancement is also an integral part of elkhorn and staghorn recovery through

restoration, restocking, and active management. Finally, ecosystem-level actions are necessary to improve habitat quality and restore keystone reef species and functional processes such as herbivory to sustain adult colonies and enable successful natural recruitment in the long term.

Recovery Goal, Objectives, and Criteria: The goal of this recovery plan is to increase the abundance and to protect the genetic diversity of elkhorn and staghorn coral populations throughout their geographical ranges while sufficiently abating threats to warrant delisting of both species. The goal, objectives, and criteria represent our expectation of what is needed to remove these two coral species from the list of endangered and threatened species. Recovery criteria can be viewed as targets, or values, by which progress toward achievement of recovery objectives can be measured. The Population-based Recovery Criteria (Criteria 1-3) represent what recovered species would look like. The Threat-based Recovery Criteria (Criteria 4-10) represent the conditions needed to abate the impacts of threats identified as contributing to the species' threatened status and allow them to sustain a recovered status. The Recovery Criteria are based on the current literature, identified assumptions, and expert consensus. In some cases, the ART was able to define quantitative Recovery Criteria because supporting information, such as models or data, was available. In some cases, the current best available information was so limited that it was not practicable to identify delisting criteria. Thus, interim criteria were identified to obtain the information necessary to establish the criteria associated with certain recovery objectives.

Recovery under the ESA is an iterative process with periodic required analyses to provide feedback into species' listing status and progress toward recovery. The ESA requires a review of the status of each listed species at least once every five years after it is listed. Periodic review of the species may lead to updates or revisions of the recovery plan, changes in the listing status of the species, or delisting. While meeting all of the recovery criteria would indicate that the species should be delisted, it is possible that delisting could occur without meeting all of the recovery criteria if the best available information indicated that the species no longer met the definition of endangered or threatened. In the case of elkhorn and staghorn corals, it is possible that because of the interaction between the threats and the species' population responses, fully achieving all of the Threat-based Recovery Criteria may not be necessary to achieving restored, sustainable populations if the benefits to the species from successfully addressing one threat (e.g., nutrient enrichment) make them more highly resilient to another threat (e.g., disease). Changes to the species' status and delisting would be made through additional rule-making after considering the same five ESA factors considered in listing decisions, taking new information into account.

Population-Based Recovery Objectives and Criteria

Objective 1: Ensure Population Viability

The recovery strategy for elkhorn and staghorn corals requires simultaneous increases in recruitment and abundance of large colonies while maintaining genetic diversity. The following criteria are population-based and measure whether stable, abundant, and genetically diverse populations of elkhorn and staghorn corals are present throughout their geographic ranges.

Criterion 1: Abundance

Elkhorn coral: Throughout approximately 10 percent of consolidated reef habitat in 1 to 5 m water depth within the forereef zone, achieve a density of 0.25 colonies ≥ 1 m diameter in size per m^2, or achieve approximately 60 percent live elkhorn coral cover. Populations with these characteristics should be present throughout the range and maintained for 20 years;

and

Staghorn coral:

Throughout approximately 5 percent of consolidated reef habitat in 5 to 20 m water depth within the forereef zone, achieve a density of 1 colony ≥ 0.5 m diameter in size per m^2, or achieve approximately 25 percent live staghorn coral cover. Populations with these characteristics should be present throughout the range and maintained for 20 years.

Criterion 2: Genotypic Diversity

Maintain current overall average genotypic diversity (proportion of unique genotypes per number of colonies sampled) of approximately 0.5 across these species' range.

Criterion 3: Recruitment

Observe recruitment rates necessary to achieve Criteria 1 and 2 over approximately 20 years;

and

Observe effective sexual recruitment (i.e., establishment of new larval-derived colonies and survival to sexual maturity) in each species' population across their geographic range.

Threat-Based Recovery Objectives and Criteria

Objective 2: Eliminate or sufficiently abate global, regional, and local threats

The recovery strategy for elkhorn and staghorn corals requires simultaneous reduction in threats across their geographic range. While each threat-based criterion influences the species' viability, there are also complex interactions and inter-relationships of threats and population response, which will require evaluation as the recovery plan is implemented. The following criteria are based on the threats affecting the status of both listed coral species and measure whether each of the threats that are currently or are expected to impede recovery of these species is sufficiently abated. While meeting all of

the recovery criteria would indicate that the species should be delisted, it is possible that delisting could occur without meeting all of the recovery criteria if the best available information indicated that the species no longer met the definition of a threatened species. In the case of elkhorn and staghorn corals, it is possible that because of the interaction between the threats and the species' population responses, fully achieving all of the Threat-based Recovery Criteria may not be necessary to achieving restored, sustainable populations if the benefits to the species from successfully addressing one threat (e.g., nutrient enrichment) make them more highly resilient to another threat (e.g., disease). Changes to the species' status would be made through additional rule-making after considering the same five ESA factors considered in listing decisions, taking new information into account.

Interim Criterion 4: Disease

Develop a quantitative recovery criterion through research. Based on 5 years of data, a criterion will be established to reduce the impact of disease to a level appropriate for recovery.

Criterion 5: Local and Global Impacts of Rising Ocean Temperature and Acidification

Sea surface temperatures across the geographic range have been reduced to Degree Heating Weeks less than 4;

and

Mean monthly sea surface temperatures remain below 30°C during spawning periods;

and

Open ocean aragonite saturation has been restored to a state of greater than 4.0, a level considered optimal for reef growth.

Criterion 6: Loss of Recruitment Habitat

Abundance (Criterion 1 above) addresses the threat of Loss of Recruitment Habitat because this criterion specifies the amount of habitat occupied by the two species. If Criterion 1 is met, then this threat is sufficiently abated;

or

Throughout the ranges of these two species, at least 40 percent of the consolidated reef substrate in 1-20 m depth within the forereef zone remains free of sediment and macroalgal cover as measured on a broad reef to regional spatial scale.

Interim Criterion 7: Nutrients, Sediments, and Contaminants (Land-Based Sources of Pollution)

Develop quantitative recovery criteria through research. Based on 5 years of data, criteria will be established to reduce sources of nutrients, sediments, and contaminants to levels appropriate for recovery.

Criterion 8: Regulatory Mechanisms

Adequate domestic and international regulations and agreements are adopted as necessary to ensure that all threat-based recovery criteria

are met. For example, appropriate local, state/territorial, national, international, and multi-jurisdictional efforts, agreements, and regulations are necessary to abate the threats from LBSP, physical impacts to corals, and rising ocean temperature and ocean acidification resulting from increasing atmospheric CO_2 concentrations.

Criterion 9: Natural and Anthropogenic Abrasion and Breakage

Appropriate and effective regulatory, response, restoration, and enforcement mechanisms are in place domestically and internationally for both planned and unplanned impacts. For planned impacts (e.g., marine construction), project planning should ensure no net loss of listed corals. Where natural or anthropogenic impacts do occur, an effective and complete response plan, including appropriate compensatory and site restoration, is executed.

Interim Criterion 10: Predation

Develop a quantitative recovery criterion through research. Based on 5 years of data, a criterion will be established to reduce the impact of predation to a level appropriate for recovery.

Actions Needed: Because many of the important threats to the recovery of elkhorn and staghorn corals are not directly manageable, the recovery strategy must pursue simultaneous actions to:

- Improve understanding of population abundance, trends, and structure through monitoring and experimental research.
- Curb ocean warming and acidification impacts to health, reproduction, and growth, and possibly curb disease threats, by reducing atmospheric greenhouse gas concentrations.
- Determine coral health risk factors and their inter-relationships and implement mitigation or control strategies to minimize or prevent impacts to coral health.
- Reduce locally-manageable stress and mortality sources (e.g., predation, anthropogenic physical damage, acute sedimentation, nutrients, contaminants).
- Develop and implement appropriate strategies for population enhancement, through restocking and active management, in the short to medium term, to increase the likelihood of successful sexual reproduction and to increase wild populations.
- Implement ecosystem-level actions to improve habitat quality and restore keystone species and functional processes such as herbivory to sustain adult colonies and enable successful natural recruitment in the long term.

Date of Recovery: The Recovery Team estimated that it will take approximately 400 years to achieve recovery based on the significant mitigative actions identified in this plan.

Total Cost of Recovery: Over the course of the next five years, and beyond, the total cost of recovery is not determinable given the global scale of many of the threats impeding recovery. Based on recovery actions for which we have cost estimates, a gross estimate for the total cost of recovery actions to be implemented in U.S. jurisdictions is calculated to be $253,540,000+. This represents an extreme

underestimate for the actual cost of recovery, which is likely to be higher in consideration of actions needed in foreign nations with elkhorn and staghorn corals living within their territorial sea outside U.S. jurisdiction.

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I. BACKGROUND

The overall goal of the Endangered Species Act (ESA) is to provide a means by which endangered and threatened species and the ecosystems upon which they depend may be conserved. To help achieve this goal, the ESA requires the preparation of a recovery plan for each listed species unless such a plan will not promote its conservation.

Recovery plans guide the implementation of actions required to recover listed species to the point at which they are self-sustainable in the wild and can be safely removed from the list of endangered and threatened species. Recovery plans are advisory documents only, and their recommendations are not obligatory. However, failure to implement recovery actions may result in the indefinite listing of the species or its extinction. This recovery plan covers both elkhorn *(Acropora palmata)* and staghorn *(A. cervicornis)* corals, which the National Marine Fisheries Service (NMFS) listed as threatened under the ESA in May 2006.

A. Brief Overview

The genus *Acropora* is the most abundant and species-rich group of corals in the world. Elkhorn and staghorn corals are two of three acroporids that are found in the Atlantic/Caribbean, typically in shallow water on reefs; the third acroporid is a hybrid of elkhorn and staghorn corals, known as fused-staghorn coral *(A. prolifera)*. Relative to other corals, both elkhorn and staghorn corals have high growth rates that have allowed acroporid reef growth to keep pace with past changes in sea level (Fairbanks 1989, Pandolfi and Jackson 2006, Blanchon et al. 2009). Both coral species were historically among the most dominant framework-building species on Atlantic/Caribbean coral reefs. Based on existing quantitative data, declines in their abundance have been estimated at 97 percent.

All scleractinian[1] corals, including elkhorn and staghorn corals, are included in Appendix II of the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES). This listing allows commercial trade and scientific exchange of specimens, but exporting countries must issue a CITES permit for international transport based on legal acquisition and a finding of non-detriment.[2]

Section 4(f)(1) of the ESA mandates that, when developing and implementing recovery plans, priority be given to species that are most likely to benefit from such plans. Therefore, NMFS assigns a recovery priority number to each listed species shortly after making a final listing determination. The recovery priority number for listed species is based on the criteria in the Recovery Priority Guidelines (NMFS 1990) and indicates the priority of each listed species for recovery plan development and implementation. Recovery priority numbers range from a high of 1 to a low of 12, based on the magnitude of threats (high, moderate, or low), recovery potential (high or low), and conflict with development projects or other economic activity. Elkhorn and staghorn corals both have a recovery priority number of 3, based on the magnitude of threats being “high,” recovery potential being “low-moderate,” and the potential for economic conflicts while implementing recovery actions.

1. Listing History

On March 4, 2004, the Center for Biological Diversity (CBD) petitioned NMFS to list three *Acropora* species — elkhorn, staghorn, and fused-staghorn *(A. prolifera)* corals — as either threatened or

[1] Underlined words are defined in the glossary, see Appendix B.
[2] A CITES permit is not required for dead coral specimens less than 30 mm (1.3 in) in size.

endangered under the ESA, and to designate critical habitat. On June 23, 2004, NMFS made a positive 90-day finding (NMFS 2004) that CBD presented substantial information indicating that the petitioned actions may be warranted. NMFS announced the initiation of a formal status review and convened an Atlantic *Acropora* Biological Review Team (BRT). The status review (available at http://sero.nmfs.noaa.gov/pr/esa/acropora.htm) concluded that disease, temperature-induced bleaching, and physical damage from hurricanes were the greatest threats to elkhorn and staghorn corals. Additionally, the threats from anthropogenic physical damage (e.g., vessel groundings, anchors, divers, and snorkelers), coastal development, competition, and predation were deemed to be moderate.

On March 3, 2005, NMFS made a determination that both elkhorn and staghorn corals are likely to become in danger of extinction throughout all or a significant portion of their range in the foreseeable future. The major stressors identified at the time as affecting the status of the two species were disease, elevated sea surface temperature, and hurricanes. Other stressors identified as contributing to the status of the species, given their extremely reduced population sizes, were sedimentation, anthropogenic abrasion and breakage, competition, excessive nutrients, predation, contaminants, loss of genetic diversity, African dust, elevated carbon dioxide levels, and sponge boring. Furthermore, NMFS concluded that listing fused-staghorn coral as threatened was not warranted, as it is a hybrid of elkhorn coral and staghorn coral and does not constitute a species as defined in the ESA. NMFS relied on the status review developed by the BRT in coming to these conclusions. After publishing a proposed rule in May 2005 and reviewing public comments received during the public comment period for the proposed rule, NMFS published a final rule listing elkhorn and staghorn corals as threatened under the ESA on May 9, 2006 (NMFS 2006).

Since the final threatened listing in 2006, new information on the status and threats to these species led the recovery team to conclude that some of the threats identified in that listing are not significantly contributing to the extinction risk status of these species. As will be explained in the sections below, recovery criteria are not needed for some of these threats.

On December 7, 2012, NMFS proposed to reclassify the status of elkhorn and staghorn corals from threatened to endangered (77 FR 73220, NMFS 2012). This proposal was based on new information on vulnerability of these two species to threats, particularly ocean acidification, and continued population declines since the original listing in 2006. Documented recruitment failure in some populations, genetic information on the percentage of clones, and the susceptibility and exposure of *Acropora* species to threats, all contributed to the proposal to reclassify the status of elkhorn and staghorn corals as endangered. In September 2014, NMFS published a final rule that maintained elkhorn and staghorn corals as threatened, instead of the proposed reclassification to endangered. The final listing rule explains NMFS' finding that these species are likely to become in danger of extinction over the next several decades due to the threats described in this recovery plan as impeding their recovery, and thus these corals continue to meet the definition of threatened species.

2. Recovery Planning and Scope

NMFS assembled the *Acropora* Recovery Team (ART) in September 2006. The team used the threats and causal listing factors that were identified in the final listing rule and new information on current threats to develop the recovery strategy (objectives, measurable criteria, and recovery actions) for these species. These objectives, measurable criteria, and recovery actions represent our expectation of what is needed to remove these two coral species from the list of endangered and threatened species; however, any of the objectives, measurable criteria, and recovery actions may be changed based on new information. Additionally, the status of listed species is reviewed every five years, a process that may include recommended changes to the recovery plan.

Only populations of elkhorn and staghorn corals that are under U.S. jurisdiction are protected under the ESA; however, recovery is required throughout the geographic ranges of these species for delisting. Additionally, many threats that these species face are global or regional in scale, and abatement of these threats within U.S. jurisdictions alone will not be sufficient for recovery. Therefore, elkhorn and staghorn coral populations that exist outside U.S. jurisdiction are considered in this plan, and recovery of elkhorn and staghorn corals will require the involvement of and cooperation with foreign nations throughout the Atlantic/Caribbean region.

B. Taxonomy and Description

PHYLUM CNIDARIA (COELENTERATA)

CLASS ANTHOZOA Ehrenburg, 1834

Subclass Zoantharia (Hexacorallia)

Order Scleractinia Bourne, 1900

Family Acroporidae Verrill, 1902

The family Acroporidae includes the genera *Montipora* (Blainville 1830), *Anacropora* (Ridley 1884), *Astreopora* (Blainville 1830), and *Acropora* (Oken 1915). Presently 368 named *Acropora* species (world-wide) are known from the literature (Veron 1986); of these only two species (elkhorn and staghorn corals) and one hybrid (fused-staghorn coral) occur in the western Atlantic and Caribbean.

Species of *Acropora* exhibit an extremely wide breadth of growth forms (e.g., staghorns, bushes, plates, tables, columns). All species contain zooxanthellae in their soft tissue. *Acropora* have a paleontological history dating from the Eocene (33 to 55 million years ago). Veron (2000) divided the genus into groups of species based on colonial morphology: for example, species with solid plates, thick table-like branches, and irregular branching with prominent axial corallites.

Staghorn coral is characterized by antler-like colonies with straight or slightly curved, cylindrical branches. The diameter of staghorn coral branches ranges from 0.25 to 5 cm (0.10 to 2 in), and tissue color ranges from golden yellow to medium brown. The growing tips of staghorn coral tend to be lighter or lack color (See Figure 1). Today, staghorn coral colonies typically exist as isolated branches and small thickets, 0.5 to 1 m (1.6 to 3 ft) across in size, unlike the vast thickets of staghorn commonly found during the 1970s.

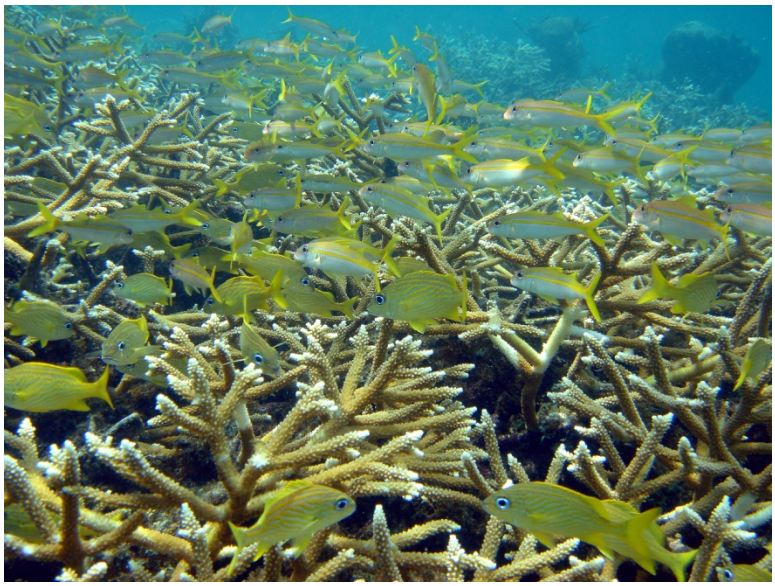

Figure 1. Staghorn coral. Photo credit: Caroline Rogers

Elkhorn coral is the largest acroporid coral found in the Atlantic/Caribbean. Colonies develop frond-like branches, which appear flattened to near round. Branches are up to 50 cm (20 in) across and range in thickness from 4 to 5 cm (1.6 to 2 in). Like staghorn coral, branches are white near the growing edges, and brown to tan away from the growing area. Individual colonies can grow to at least 2 m (6.5 ft) in height and 4 m (13 ft) in diameter (See Figure 2).

Figure 2. Elkhorn coral. Photo credit: Michael Barnette.

C. Distribution and Habitat Use

1. Distribution

Elkhorn and staghorn corals are widely distributed throughout the western Atlantic, Caribbean, and Gulf of Mexico, both inside U.S. jurisdiction (Florida, Puerto Rico, U.S. Virgin Islands (USVI), Texas (Flower Garden Banks National Marine Sanctuary), Navassa) and outside U.S. jurisdiction (Anguilla, Antigua and Barbuda, Aruba, Bahamas, Barbados, Belize, British Virgin Islands, Cayman Islands, Colombia, Costa Rica, Cuba, Dominica, Dominican Republic, Grenada, Guadeloupe, Haiti, Honduras, Jamaica, Monserrat, Martinique, Mexico, Netherlands Antilles, Nicaragua, Panama, St. Barthelemy, St. Kitts and Nevis, St. Lucia, St. Vincent and the Grenadines, Trinidad and Tobago, Turks and Caicos, and Venezuela). The best scientific data available show the current general geographical distribution of elkhorn and staghorn corals has remained unchanged from the historical (no evidence of range constriction) (see Figure 3), though the percentage of reefs where the two species were historically present has declined (Jackson et al. 2014).

Figure 3. Approximate range of elkhorn and staghorn corals (highlighted), including the Gulf of Mexico, Atlantic Ocean, and Caribbean Sea. The highlighted areas are not specific locations of the corals, but rather reflect general distributions (*Acropora* BRT 2005).

The geographic area occupied by listed coral species that is within the jurisdiction of the United States is limited to four counties in the State of Florida (Palm Beach County, Broward County, Miami-Dade County, and Monroe County), Flower Garden Banks National Marine Sanctuary (FGBNMS), and the U.S. territories of Puerto Rico, USVI, and Navassa Island.

In Florida, staghorn coral has been documented along the east coast as far north as Palm Beach, occurring in deeper water (16 to 30 m; 53 to 98 ft) at its northernmost range (Goldberg 1973, Tichenor pers. comm.), and distributed across its depth range (5-30 m) moving south and west throughout the coral and hardbottom habitats off Broward County (where it forms extensive thickets), Miami-Dade County, the Florida Keys, and the Dry Tortugas (Jaap 1984). Fossil elkhorn coral reef framework extends from Palm Beach County throughout the Florida Keys and discontinuously to the Dry Tortugas. Living elkhorn coral is relatively scarce offshore of Broward and Miami-Dade Counties, and is more common southward.

Coral reefs with varying densities of elkhorn and staghorn corals are present in Puerto Rico off all coasts of the main island and around some of its smaller islands. Where surveys have been conducted, dense, high profile thickets of elkhorn and staghorn corals are present in only a few reefs along the southwest, north, and west shore of the main island and isolated offshore locations (Schärer et al. 2009, Weil et al. unpublished data, Hernandez unpublished data). In addition to live colonies, large stands of dead elkhorn currently exist on the fringing coral reefs along the shoreline (e.g., Punta Picúa, Punta Miquillo, Río Grande, Guánica, La Parguera, and Mayagüez).

USVI reefs also support populations of elkhorn and some staghorn corals. The geographic information system (GIS) data NMFS has received indicate the presence of elkhorn and staghorn corals around most of St. Croix, but given the presence of coral reef and colonized hardbottom habitats surrounding the entire island, it is possible unrecorded colonies exist where data are not available (e.g. southwestern shore). Mayor et al. (2006) recorded elkhorn colony presence in Buck Island National Monument and found higher densities in the northern and eastern areas around the island. There are limited quantitative data of presence of either species off the islands of St. Thomas; however, anecdotal reports of both species have been reported. There are several areas around the island of St. John that support healthy populations of both elkhorn (Grober-Dunsmore et al. 2006) and staghorn corals; however, the elkhorn coral populations underwent serious decline during the 2005 bleaching event. Little information is available on changes in staghorn coral populations around St. John (Rogers pers. comm.). The data NMFS has indicate that there is coral reef and colonized hard bottom habitat surrounding each of these islands, as well as the smaller offshore islands of USVI. Again, it is possible that unrecorded colonies are present in these offshore island areas.

Navassa Island is a small, uninhabited, oceanic island approximately 50 km (31 mi) off the southwest tip of Haiti that is managed by U.S. Fish and Wildlife Service (FWS) as one component of the Caribbean Islands National Wildlife Refuge (NWR). Both listed coral species are known from Navassa, with elkhorn coral apparently increasing in abundance since 2000, and staghorn coral rare and declining (Miller et al. 2008a).

Last, there are two known colonies of elkhorn coral at FGBNMS, located 161 km (100 mi) off the coast of Texas in the Gulf of Mexico. The FGBNMS is comprised of three areas of salt domes that rise to approximately 15 m (50 ft) from the surrounding water depth of 61 to 122 m (200 to 400 ft). The FGBNMS is regularly surveyed, and the two known colonies were discovered only recently in 2003 and 2005 (Zimmer et al. 2006).

2. Habitat Use

Elkhorn and staghorn coral naturally occur on spur and groove, bank reef, patch reef, and transitional reef habitats, as well as on limestone ridges, terraces, and hardbottom habitats (Goldberg 1973, Gilmore and Hall 1976, Cairns 1982, Davis 1982, Jaap 1984, Wheaton and Jaap 1988, Miller et al. 2008b). Staghorn coral commonly grows in water ranging from 5 to 20 m (16 to 60 ft) in depth but has rarely been found to 60 m (197 ft) (Wells 1933, Davis 1982, Jaap 1984, Jaap and Wheaton 1988, Jaap et al. 1989). Although staghorn coral colonies are sometimes found interspersed among colonies of elkhorn coral, they are generally located in deeper water seaward of the elkhorn coral zone and, hence, in waters more protected from waves. Today staghorn corals in the Florida Keys occur primarily in patch reefs as opposed to their former abundance in deeper forereef habitats (Miller et al. 2008b). Historically, staghorn coral was one of the primary constructors of mid-depth (10 to 15 m; 33 to 49 ft) reef terraces in the western Caribbean, including Jamaica, the Cayman Islands, Belize, and some reefs along the eastern Yucatan peninsula (Adey 1978).

Elkhorn coral commonly grows in turbulent shallow water on the fore reef, reef crest, and shallow spur and groove zone (Shinn 1963, Cairns 1982, Rogers et al. 1982, Miller et al. 2008b) in water ranging from 1 to 5 m (3 to 16 ft) in depth but has been found to 30 m (98 ft) depth and in back reef environments. Colonies of elkhorn coral often grow in nearly mono-specific, dense stands and form an interlocking framework known as thickets in fringing and barrier reefs (Jaap 1984, Tomascik and Sander 1987, Wheaton and Jaap 1988; see Figure 4). In addition, fragments often accumulate on shore (where they may form islands), and at the base of the reef. Elkhorn coral formed extensive barrier-reef structures in Belize (Cairns 1982), the greater and lesser Corn Islands, Nicaragua (Lighty et al. 1982), and Roatan,

Honduras, and built extensive fringing reef structures throughout much of the Caribbean (Adey 1978). Colonies generally do not form a thicket below a depth of 5 m (16 ft), with maximum water depths of framework construction ranging from 3 to 12 m (10 to 39 ft) (Lighty et al. 1982).

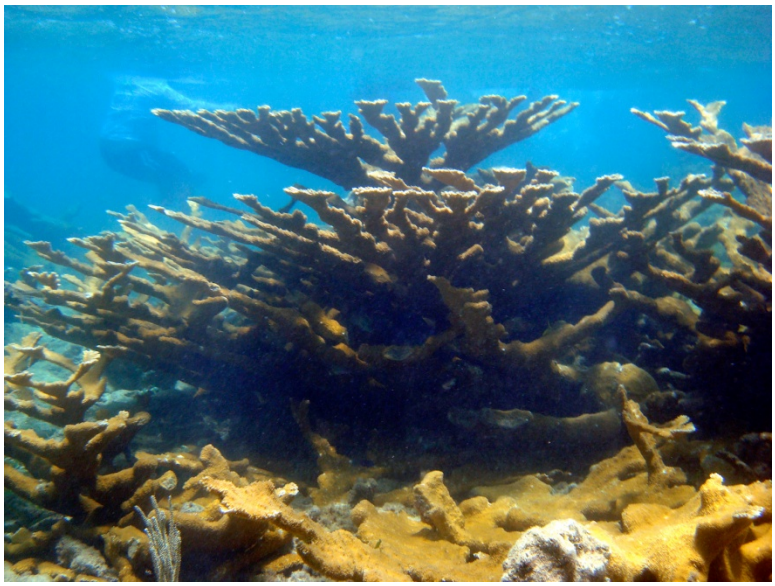

Figure 4. Elkhorn thicket off Vega Baja, Puerto Rico. Photo Credit: NOAA Restoration

Appropriate habitat that supports growth and reproduction of elkhorn and staghorn corals typically consists of consolidated substrate (i.e., stable, dead coral skeleton or hardbottom), which is required for successful settlement of larvae and reattachment of fragments. The type of substrate available directly influences settlement success and fragment survivorship (Lirman 2000). Additionally, both species require relatively clear, well-circulated water (Jaap et al. 1989) and are highly dependent upon sunlight for nourishment (Porter 1976, Lewis 1977). Unlike other coral species, neither elkhorn nor staghorn coral is likely to compensate for reductions in long-term water clarity with alternate food sources, such as zooplankton and suspended particulate matter (*Acropora* BRT 2005). Typical water temperatures in which these coral species grow range from 21° to 30°C (70 to 84°F), but they are able to tolerate temperatures both lower and higher than the seasonal minimum/maximum for a brief period of time. Their responses to temperature perturbations depend on the duration and intensity of the exposure as well as other biological and environmental factors.

D. Critical Habitat

The ESA requires that NMFS and FWS designate critical habitat for species that have been listed as threatened or endangered. Designation of critical habitat must occur in a public rule-making process within a specific timeframe and must use the best scientific information available. The ESA defines critical habitat as specific areas:

> *1) within the geographical area occupied by the species at the time of listing, on which are found physical or biological features essential to conservation, and which may require special management considerations or protection; and 2) outside the geographical area occupied by the species if the agency determines that the area itself is essential for conservation.*

Before designating critical habitat, consideration must be given to the economic impacts, impacts on national security, and other relevant impacts of specifying any particular area as critical habitat. NMFS

may exclude an area from critical habitat if the benefits of exclusion outweigh the benefits of designation, unless excluding the area will result in the extinction of the species concerned.

On November 26, 2008, NMFS designated critical habitat for elkhorn and staghorn corals (NMFS 2008). The designated areas — approximately 2,959 square miles — include marine habitat in four counties of Florida, in Puerto Rico and its associated islands, and in St. Thomas, St. John, and St. Croix, USVI (see Figure 5-8). NMFS proposed critical habitat in February 2008, held public hearings, reviewed all comments and new information provided by the public and other reviewers, and incorporated minor revisions into the final designation.

The critical habitat designation identifies the facilitation of increased incidence of successful sexual and asexual reproduction as the key objective for the conservation of listed corals. Based on the key conservation objective, the natural history of elkhorn and staghorn corals, and their habitat needs, NMFS identified the following physical or biological feature of elkhorn and staghorn coral habitat essential to their conservation (essential feature):

> *substrate of suitable quality and availability to support larval settlement and recruitment, and reattachment and recruitment of asexual fragments.*

"Substrate of suitable quality and availability" is defined as natural consolidated hard substrate or dead coral skeleton that is free from fleshy or turf macroalgae cover and sediment cover. This feature is essential to the conservation of these two species due to the extremely limited recruitment currently being observed.

To designate specific areas on which the essential feature for threatened corals is found, NMFS relied on information obtained from the public, NMFS Southeast Fisheries Science Center, NOAA National Centers for Coastal Ocean Science Biogeography Team, and the U. S. Geological Survey (USGS) of the Department of the Interior. NMFS identified four "specific areas" within the geographical area occupied by these species at the time of listing that contain the essential feature. These areas comprise all waters in the depths of 98 ft (30 m) and shallower to: (1) the 6-ft (1.8 m) contour from Boynton Inlet, Palm Beach County, to Government Cut, Miami-Dade County; and the mean low water (MLW) line from Government Cut south to 82° W longitude in Monroe Counties; and the MLW line surrounding the Dry Tortugas, Florida; (2) the MLW line in Puerto Rico and associated Islands; (3) the MLW line in St. John/St. Thomas, USVI; and (4) the MLW line in St. Croix, USVI (See Figure 5-Figure 8). Within these four specific areas, the essential feature consists of natural consolidated hard substrate or dead coral skeleton that is free from fleshy or turf macroalgae cover and sediment cover. Natural sites covered with loose sediment, fleshy or turf macroalgal covered hard substrate, or seagrasses do not provide the essential feature for elkhorn and staghorn corals. Additionally, all existing (meaning constructed at the time of the designation of critical habitat) federally-authorized or permitted man-made structures, such as aids-to-navigation (ATONs), artificial reefs, boat ramps, docks, pilings, channels, or marinas, do not provide the feature that is essential to these species' conservation. NMFS excluded one military site, the Dania Restricted Anchorage Area, comprising approximately 5.5 square miles (14.3 sq km), because of national security impacts.

ESA Section 4(a)(3)(B) prohibits designating as critical habitat any lands or other geographical areas owned or controlled by the Department of Defense, or designated for its use, that are subject to an Integrated Natural Resource Management Plan (INRMP), if NMFS determines that such a plan provides a benefit to these coral species (16 U.S.C. 1533(a)(3)(B)). NMFS determined that the Naval Air Station Key West (NASKW) INRMP provides a benefit to the two corals. Therefore, NMFS did not designate critical habitat within the boundaries covered by the NASKW INRMP.

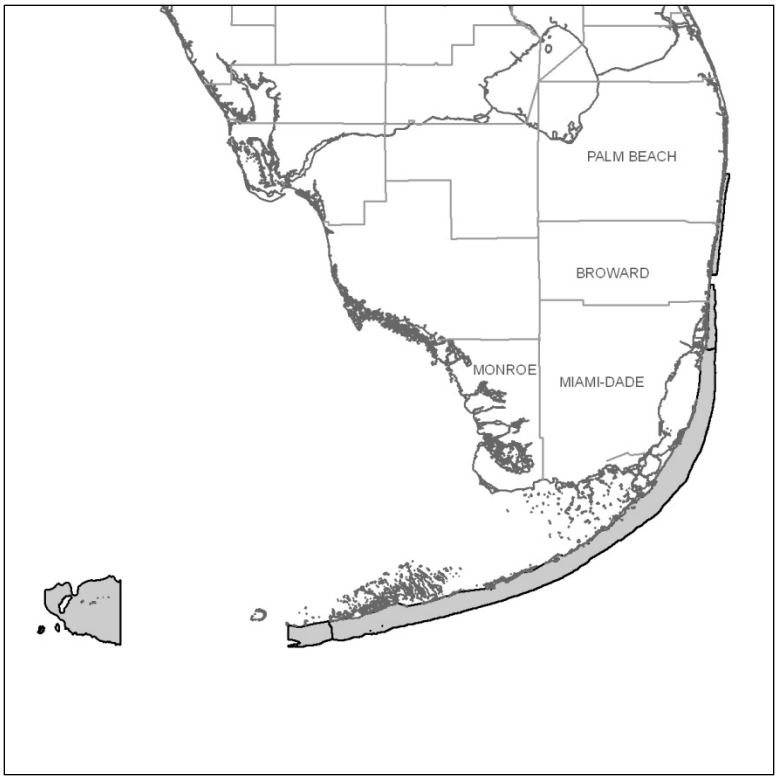

Figure 5. Florida Critical Habitat Area.

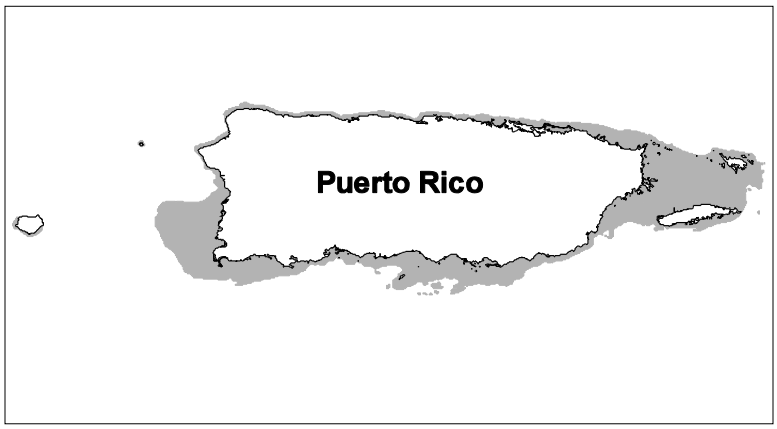

Figure 6. Puerto Rico Critical Habitat Area.

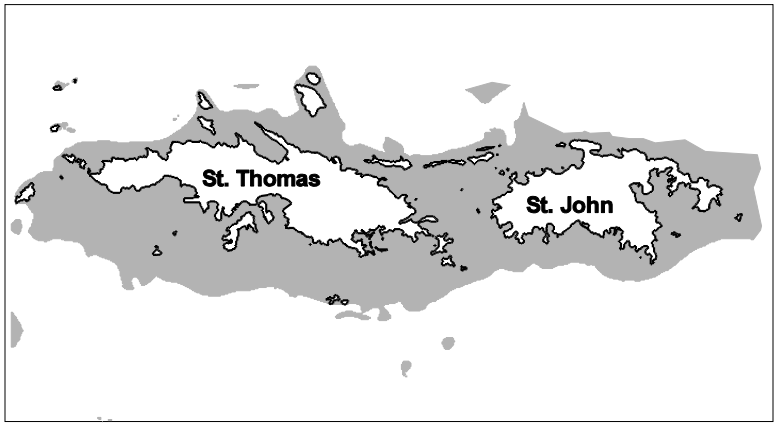

Figure 7. St. John/St. Thomas Critical Habitat Area.

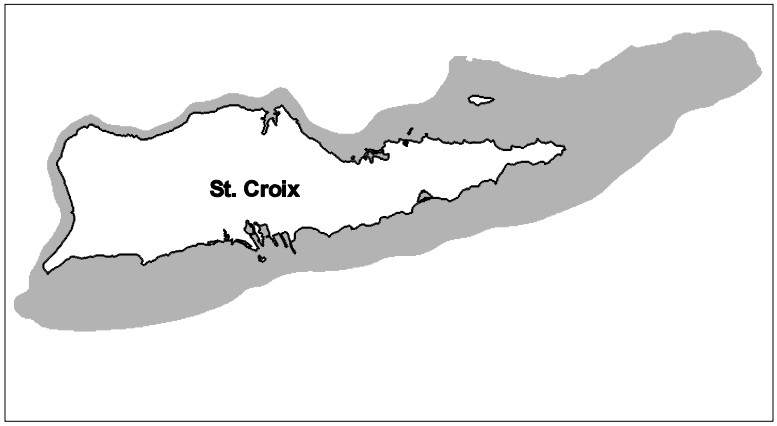

Figure 8. St. Croix Critical Habitat Area.

E. Life History

1. Age and Growth

The skeletal growth rate for staghorn coral has been reported to range from 3 to 11.5 cm/yr (1 to 5 in/yr) (Vaughan 1915, Shinn 1966, Jaap 1974, Shinn 1976, Gladfelter et al. 1978, Becker and Muller 2001). This growth rate is relatively fast in comparison to other scleractinian corals and historically enabled these species to construct significant reef structures in several locations throughout the Atlantic/Caribbean (Adey 1978). During daylight, calcium carbonate ($CaCO_3$) accretion occurs on all of the skeletal elements of staghorn coral; at night the activity is limited to crystal formation at the extending tips of skeletal elements. Gladfelter (1983) reported daily linear extension tissue growth of 300 µm in the region of the axial polyp. "*Acropora cervicornis* exhibits a daily rhythm in calcification capacity, with daily maxima at sunrise and sunset. Daily minima occur shortly after sunrise and sunset" (Chalker 1977).

Population growth in staghorn coral occurs predominantly via asexual reproduction. Asexual reproduction involves fragmentation, wherein colony pieces or fragments break from a larger colony and re-attach to hard, consolidated substrate to form a new colony (see section 3. Reproductive

Biology). A broken-off branch (i.e., fragment) may land close to the original colony or be moved a short distance by waves. If the location is favorable, fragments grow into a new colony, expanding into and occupying additional area. Fragmentation, coupled with a relatively fast skeletal growth rate, facilitates potential spatial competitive superiority for staghorn coral relative to other corals and other benthic organisms (Shinn 1976, Neigel and Advise 1983, Jaap et al. 1989).

The skeletal growth rate for elkhorn coral, expressed as the linear extension of branches, is reported to range from 4 to 11 cm/year (1.6 to 4.3 in/year) (Vaughan 1915, Jaap 1974, Gladfelter, et al. 1978, Garcia et al. 1996, Becker and Mueller 2001). Annual linear extension has been found to be dependent on the size of the colony (Padilla and Lara 1996), and new recruits and juveniles typically grow at slower rates. Additionally, stressed colonies and fragments may also exhibit slower growth. For example, some fragments at the *Fortuna Reefer* vessel grounding site at Mona Island, Puerto Rico failed to show any measurable growth over ten years (Bruckner et al. 2008). Wells (1933) reported from observations in 1932 that colonies of elkhorn coral were 2.4 m (8 ft) high and 4.5 m (15 ft) in diameter at Bird Key Reef, Dry Tortugas. However, colonies up to approximately 7 m (21 ft) in diameter have been observed (Gladfelter pers. comm.).

Elkhorn coral populations can expand via repeated cycles of fragmentation. A branch of elkhorn coral may be carried by waves and currents away from the parent colony, and fragments cleaved from the colony may grow into new colonies (Highsmith et al. 1980, Bak and Criens 1982, Highsmith 1982, Rogers et al. 1982). Genetically identical clones have been found separated by distances that range from 0.1 to 100 m (0.3 to 328 ft), but usually less than 30 m (98 ft) (Baums et al. 2006). Fragmentation during storm events is a significant means of generating new colonies as documented during several storms: Hurricanes Hattie (Stoddart 1962, 1969), Edith (Glynn et al. 1964), Gerta (Highsmith et al. 1980), Allen (Woodley et al. 1981), David and Frederic (Rogers et al. 1982), Hugo (Bythell et al. 1993), Joan (Geister 1992, Zea et al. 1998), Gilbert (Kobluk and Lysenko 1992; Jordan-Dahlgren and Rodriguez-Martinez 1998), and Andrew (Lirman and Fong 1996, Lirman and Fong 1997), as well as after Tropical Storms Bret (Van Veghel and Hoetjes 1995) and Gordon (Lirman and Fong 1997). Lirman and Fong (1997) reported that elkhorn coral fragment wounds healed rapidly (1.59 cm of linear growth/month; 0.62 in/month). Nine months after Tropical Storm Gordon, 157 of 218 fragments had fused to the sea floor, and proto-branches on the fragments grew rapidly.

2. Diet and Feeding Behavior

Elkhorn and staghorn corals are highly dependent upon sunlight for nourishment compared to massive, boulder-shaped species in the region which obtain a relatively higher proportion of their energy needs from the capture of zooplankton (Porter 1976, Lewis 1977). Thus, elkhorn and staghorn corals are likely very susceptible to increases in water turbidity. Decreases in long-term water clarity can also reduce the coral production to respiration ratio below one, meaning the colony is using more energy than is created by the zooxanthellae. Elkhorn and staghorn corals may not be able to compensate with an alternate food source, such as zooplankton and suspended particulate matter, like other corals. Elkhorn and staghorn corals also may not be as resilient following bleaching events as corals that are able to compensate with other food sources (Grottoli et al. 2006).

3. Reproductive Biology

Sexual Reproduction

Elkhorn and staghorn corals reproduce both sexually and asexually. Neither coral differs substantially from the other in terms of sexual reproductive biology. Both species are broadcast spawners, meaning that gametes are released into the water column (Szmant 1986). Additionally, both species are

simultaneous hermaphrodites, meaning that a given colony will produce both eggs and sperm. However, two genetically distinct parents are required to produce viable larvae (Baums et al. 2005a). Consequently, some large thickets of healthy corals may have limited sexual reproductive potential if they are composed only of one or few genetic individuals. The spawning season for elkhorn and staghorn corals is relatively short, with gametes released on only a few nights (nights 2-6 after the full moon) during July, August, or September. Timing of spawning also may depend on latitude, occurring in a later month (e.g., October) in the southern Caribbean, and some populations may have two spawning events over the course of two months. Large elkhorn and staghorn corals produce proportionally more gametes than small colonies since basal and branch tip tissue are not fertile (Soong and Lang 1992).

In elkhorn and staghorn corals, fertilization and development is exclusively external to the parental colonies. Embryonic development culminates with the development of planktonic larvae called planulae. Coral planula larvae experience very high mortality from predation or other factors during their planktonic phase (Goreau et al. 1981). Little is known concerning the settlement patterns of planula larvae of elkhorn and staghorn corals in the wild. In general, upon proper stimulation, coral larvae, whether brooded inside parental colonies or developed in the water column external to the parental colonies (like elkhorn and staghorn corals), settle and metamorphose on appropriate substrates. Like most corals, elkhorn and staghorn corals require hard, consolidated substrate, including stable, dead coral skeleton, for their larvae to settle upon. Certain species of crustose coralline algae have been shown to facilitate settlement and post-settlement survival in both staghorn and elkhorn coral, while other species do not (Ritson-Williams et al. 2009). Although unverified in the field, laboratory experiments suggest elkhorn planulae may prefer to settle on upper, exposed surfaces rather than under surfaces like many other coral species (Szmant and Miller 2005). Because newly settled corals barely protrude above the substrate, juveniles need to reach a minimum size to escape damage or mortality from grazing, sediment burial, and algal overgrowth. Recent studies examined early survivorship in the Florida Keys by settling elkhorn coral larvae onto experimental limestone plates in the laboratory, then placing these plates out in the field. The results indicate that elkhorn coral had substantially higher survivorship than another spawning coral species, *Orbicella* (formerly *Montastraea*) *faveolata*, but much lower survival than brooding coral species over the first nine months following settlement (Szmant and Miller 2005).

Successful recruitment of larvae (i.e., sexual recruitment) is the only means by which new genetic individuals enter a population, thereby maintaining or increasing genotypic diversity. Planula larvae are also important as the only phase in the life cycle of elkhorn and staghorn corals that disperse over long distances, genetically linking populations and providing potential to re-populate depleted areas. Baums et al. (2005a) examined genetic exchange in elkhorn coral by sampling and genotyping colonies from eleven locations throughout its geographic range using microsatellite markers. Results indicate that elkhorn populations in the eastern Caribbean (St. Vincent and the Grenadines, USVI, Curacao, and Bonaire) have experienced little or no genetic exchange with populations in the western Atlantic/Caribbean (Bahamas, Florida, Mexico, Panama, Navassa, and Mona Island). Puerto Rico is an area of mixing where elkhorn populations show genetic contribution from both regions, though it is more closely connected with the western Caribbean. Within these regions, the degree of larval exchange appears to be asymmetrical with some locations being entirely self-recruiting and some receiving immigrants from other locations within their region.

Using seven microsatellite markers, Baums et al. (2010) examined 278 staghorn coral samples from Florida and five regions in the Caribbean. They found that the population across Florida showed no discernible genetic structure but was distinct from the other areas in the Caribbean, as was Honduras. Individual genotypes in St. Thomas, USVI and Puerto Rico belonged to the same population as did

genotypes from Navassa and the Bahamas. Vollmer and Palumbi (2007) examined multilocus sequence data from 276 colonies of staghorn coral spread across 22 populations from 9 regions in the Caribbean, Florida, and the Bahamas. Their data were consistent with the West-East Caribbean subdivision observed in elkhorn coral populations by Baums et al. (2005b); however staghorn coral showed more population subdivision than elkhorn coral (Baums et al. 2010). Additionally, data from the Vollmer and Palumbi (2007) study indicated that regional populations of staghorn coral separated by greater than 500 km (310 mi) are genetically differentiated and that gene flow across the greater Caribbean is low overall. This is consistent with studies conducted on other Caribbean corals showing that gene flow is restricted at spatial scales over 500 km (310 mi) (Fukami et al. 2004; Baums et al. 2005b; Brazeau et al. 2005). Furthermore, fine-scale genetic differences were observed among reefs separated by as little as 2 km (1.2 mi), suggesting that gene flow in staghorn corals may be limited over much smaller spatial scales (Vollmer and Palumbi 2007). Both acroporid population studies suggest that no population is more or less significant to the status of these species and there is limited ability of reefs to seed one another over large distances.

Asexual Reproduction

Elkhorn and staghorn corals also reproduce asexually. Asexual reproduction involves fragmentation, wherein colony pieces or fragments break from a larger colony and re-attach to hard, consolidated substrate to form a new colony. Various types of physical disturbance (e.g., storms or ship groundings) usually initiate fragmentation, but other factors such as bioerosion of the skeleton may make branches more prone to break. Reattachment occurs when either live coral tissue on the fragment grows onto suitable substrate or encrusting organisms settle on the dead basal areas of the fragment and cement it to the adjacent substratum (Tunnicliffe 1981). Fragmentation results in multiple colonies that are genetically identical (ramets or clones) while sexual reproduction results in the creation of new genotypes (genets).

Genetic sampling shows that elkhorn coral populations have had considerable geographic variation in the relative contribution of sexual versus asexual reproduction (Baums et al. 2006). Fragmentation can play a major role in maintaining local populations when sexual recruitment is very limited. The larger size of fragments compared to planulae may result in higher survivorship after recruitment (Jackson 1977). Also unlike sexual reproduction, which is restricted seasonally (Szmant 1986), fragmentation can take place year-round. However, potential consequences of high clonality include poor to no reproductive success (because elkhorn and staghorn corals do not self-fertilize) and potential increased susceptibility to stress events for which that clone is not adapted. Additionally, severe fragmentation, as commonly observed after storms, may limit future sexual reproduction by reducing the biomass of colonies and shifting the energy allocation of damaged colonies from reproduction to regeneration. Last, the size and weight of fragments limit their dispersal range (Jackson 1986, Lirman 2000), slowing the recovery of damaged areas where the cover of adult colonies (i.e., fragment source) has been reduced significantly (Baums et al. 2006).

4. Life History Information Limitations

Our knowledge of the biology and life history of both elkhorn and staghorn corals is limited by several factors, including current and historical distribution and abundance patterns, changes that have occurred over different time scales, and the factors influencing the trajectory of extant populations. More demographic data and modeling tools are needed to predict the response of populations to future disturbances and stressors at various spatial and temporal scales. An elkhorn coral population model has been developed based on demographic monitoring from several locations throughout the species'

range (Vardi 2011). Preliminary results from various runs of the model informed the ART in the development of this plan.

During the critical habitat designation process, NMFS collected GIS and remote sensing data on the presence/absence of elkhorn and staghorn corals, benthic habitat, water depth, and water temperature; however, these data are limited spatially (i.e., not all areas have been mapped) and temporally (i.e., some data sets are outdated). Furthermore, understanding of reproductive and recruitment processes and the importance of population structure and genetics for both elkhorn and staghorn corals is limited. The following are inadequately understood and require additional scientific information:

- The relative importance of sexual versus asexual reproduction in populations and factors determining variation;
- Spatial and temporal variability in gamete production, release, and fertilization;
- Transport and duration of larval stages and factors affecting planktonic larval survivorship;
- Environmental requirements and preferences for larval settlement, post-settlement survivorship, and growth to maturity.

F. Abundance and Trends

Historically, elkhorn and staghorn corals were dominant coral species and principle contributors to reef accretion in the Atlantic/Caribbean. Both species commonly formed vast mono-specific thickets, lending their names to distinct zones in classical descriptions of Caribbean reef morphology (Goreau 1959), with elkhorn coral dominating in shallow reef crest habitats (less than 5 m (16 ft) depth) and staghorn coral thickets more common in forereef shelf areas (7-15 m depth; 23-49 ft). Given the clonal nature of these species, their historically ubiquitous status, and the tendency for colonies to grow together to form complex thickets, few historical estimates for elkhorn or staghorn coral colony abundance are available.

Caribbean-wide, massive reductions in percent cover, dominance, and presence of elkhorn and staghorn corals occurred during the 1970s and 1980s. Since this major die-off, percent cover has remained relatively stable at the reduced levels throughout the Caribbean (Jackson et al. 2014). Existing quantitative estimates for population reductions, in areas where they are available, range up to 98 percent at the time of the first status review (*Acropora* BRT 2005). Since 2005, additional catastrophic mortality events for elkhorn coral (e.g., 50 percent of existing, monitored populations) have been documented in localized studies due to mass-bleaching events (USVI; Muller et al. 2008, Lundgren 2008) and hurricanes/disease (Florida Keys; Williams et al. 2008). It is likely that such episodic mass-mortality events caused by bleaching, disease, and/or physical disturbances will continue in the future. While recruitment of new elkhorn and staghorn coral colonies has been reported in various geographic locations, subsequent mortality rates may be precluding increases in large, mature colonies to sizes greater than 1 m (3 ft) in colony diameter and development of thickets which contribute disproportionately to habitat structure and reef productivity (e.g., Grober-Dunsmore et al. 2007). In the Florida Keys the recovery trajectory of elkhorn coral following approximately 50 percent population reduction in the 2005 mass mortality event suggests more than ten years to recover (Williams and Miller 2012). Meanwhile, mass mortalities in this population have been observed more frequently than every 10 years (i.e., 1997-8 and 2005). Similar patterns of mass mortality (i.e., ~ 50 percent loss during hurricane Omar in 2008) and slow rates of recovery have been observed in Curaçao populations as well (Bright et al. 2013)

Based on available data, the current range for both elkhorn and staghorn corals remains unchanged from the historical; quantitative data for many locations throughout the wider Atlantic/Caribbean are lacking. It is clear that small pockets of robust population abundance/density persist in small areas.

These robust reference populations should be targeted in future assessment and eco-epidemiological analyses to determine what factors (e.g. environmental or genetic factors) are responsible for maintaining high abundance (e.g., high recruitment, high growth, low mortality) and good colony condition (e.g., low exposure to stressors versus highly resistant colonies).

G. Listing/Delisting Factors: Threats Assessment

As part of the recovery planning process, it is important to document the existence of all threats that can adversely affect the species. This recovery plan evaluates both the threats identified in the final listing rule (NMFS 2006) that were considered at the time as contributing to the species' threatened status, and new and emergent threats that may adversely affect elkhorn and staghorn corals, to determine which threats are contributing to the species' extinction risk status and thus require recovery criteria. Individual threats were assessed with regard to their geographic extent, severity, life stage affected, and responsiveness to management. The threats assessment includes consideration of both natural and human threats, which can result from either intentional or unintentional actions affecting these species either directly or indirectly. The threats assessment includes factors that may have been instrumental in these species' declines (e.g., storms or disease), factors that may not have been a root cause of initial declines in these species' populations but that may significantly impede recovery (e.g., ocean acidification or depensatory population effects), and factors that negatively affect corals but that may not impede the species' recovery if some of the larger, more severe threats are abated (e.g., boring sponges, competition). The current or potential severity of each threat is affected by a variety of characteristics including the immediate or long-term impact on these species (e.g., whether the threat is lethal or adds some stress to these species), the geographic extent of the threat (i.e., how many populations are affected), and the consideration of the specific life stage(s) affected. Generally, the greater the geographic extent of a threat, the higher the concern, and the later in life that a threat impacts these species, the greater the effect to the persistence and recovery of these species overall; however, there are exceptions to both of these generalities.

An assessment of an individual threat not only includes consideration of its severity, but also the responsiveness of that threat to potential management actions and the feasibility of implementing those actions. If no effective measures to minimize or mitigate the threat are known, no recovery actions may be available at the current time. The ability to implement management actions to address a threat and the likelihood that those actions will be effective are critical considerations when formulating a strategy for the recovery of a listed species. However, "unmanageable" threats must be fully considered in order to frame appropriate actions and expectations relative to the manageable threats.

An assessment of threats must also recognize the interrelationship among various threats. There may be additive or synergistic effects of multiple threats. For example, increasing evidence suggests that the widespread and devastating impacts of coral diseases are related to warming temperatures and/or bleaching (Muller et al. 2008, Cervino et al. 2004, Bruno et al. 2007, Brandt and McManus 2010). Additionally, individual threats may have the same source, and thus co-occur (e.g., sediments and nutrients). Evaluation of the individual threats in isolation may lead to an underestimate of their impact on elkhorn and staghorn corals. Attention must be paid to the cumulative impacts of multiple threats or interrelationships among threats in order to ensure an accurate assessment.

Table 1 lists the threats that adversely affect elkhorn and staghorn corals, as determined by the ART. The associated ESA listing factor is included for those threats that were identified in the 2006 final listing rule (NMFS 2006) and in the 2014 final rule as contributing to the species' threatened status. There are five listing factors designated by letters A-E in Table 1: A) present or threatened destruction, modification, or curtailment of habitat or range, B) over-utilization for commercial, recreational,

scientific, or educational purposes, C) disease or predation, D) inadequacy of existing regulatory mechanisms, and E) other natural or manmade factors affecting the continued existence. Some threats have multiple associated listing factors (e.g., a threat such as storms may degrade reef habitat as well as kill coral colonies directly). The table also ranks the severity of each threat on a scale of 0-5+ at the range-wide level (Atlantic/Caribbean-wide) and at local levels for each of the U.S. jurisdictions for both elkhorn (Elk) and staghorn (Stag). The severity of the threat is indicated as follows: 0-2 = low, 3 = medium, 4-5 = high, and 5+ = high and main cause of initial decline. The threats are also sorted from most severe to least severe for easy reference. There are some threats that are believed to be significant, but ranking is unknown relative to other threats (indicated by SBU) and some potential threats that are likely having minor effects at the present time but could pose a larger threat in the future (indicated by P). The table identifies whether the threat is likely to impede recovery of these species (Y or N). While all the threats listed in Table 1 adversely affect the two species, some threats (given their relatively low comparable severity) may not need to be abated in order to recover these species if other, more severe threats are abated first. The Recovery Criteria and associated Recovery Actions laid out later in the plan address only those threats that have a "Y" in the "Impedes Recovery" column of Table 1. Following the threats table is a narrative that describes each threat and how each of the individual rankings was derived. As in the table, the narratives are arranged from most severe to least severe.

Table 1. Assessment of Potential and Present Threats to Elkhorn (Elk) and Staghorn (Stag) Corals

			Range-wide		Florida Keys		Southeast Florida		Puerto Rico		USVI	
Threat/Stress	**Impedes Recovery?**	**Listing Factor**	**Stag**	**Elk**	**Stag**	**Elk**	**Stag**	**Elk**	**Stag**	**Elk**	**Stag**	**Elk**
Disease	Y	C	5+	5+	5+	5+	5+	5+	5+	5+	5+	5+
Temperature	Y	A, E	5	5	5	5	5	5	5	5	5	5
Loss of Recruitment Habitat	Y	A	4	4	4	4	4	4	4	4	4	4
Inadequacy of Existing Regulatory Mechanisms	Y	D	4	4	4	4	4	4	4	4	4	4
Natural Abrasion and Breakage of Species	Y	E	4	4	4	4	4	4	4	4	4	4
Acidification	Y	E	4	4	4	4	4	4	4	4	4	4
Depensatory Population Effects	Y	E	3	3	3	3	3	5	3	3	3	3
Sedimentation	Y	A, E	3	3	1.5	1.5	3	3	3	4	3	4
Predation	Y	C	3	3	2	3	2	2	3	4	3	3
Anthropogenic Abrasion and Breakage of Species	Y	E	2*	2*	2	2	3	2	3	3	3	3
Anthropogenic Abrasion and Breakage of Habitat	Y	A	2	2	2	2	2	2	3	3	3	3
Nutrients	Y	A, E	SBU	SBU	SBU	SBU	SBU	SBU	SBU	SBU	SBU	SBU
Contaminants	Y	E	SBU	SBU	SBU	SBU	SBU	SBU	SBU	SBU	SBU	SBU

			Range-wide		Florida Keys		Southeast Florida		Puerto Rico		USVI	
Threat/Stress	**Impedes Recovery?**	**Listing Factor**	**Stag**	**Elk**	**Stag**	**Elk**	**Stag**	**Elk**	**Stag**	**Elk**	**Stag**	**Elk**
Natural Abrasion and Breakage of Habitat	N	A	2	2	2	2	2	2	2	2	2	2
Offshore Gas and Oil Exploration	N		1	1	1.5	1.5	1.5	1.5	1	1	1	1
Sea Level Rise	N	A	1	1	1	1	1	1	1	1	1	1
Overharvest	N		1	1	1	1	1	1	1	1	1	1
Overgrowth Competition	N	E	1	1	1	1	2	1	1	1	1	1
Sponge Boring	N	E	1	1	1	1	1	1	1	2	1	1
African Dust	N	E	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Alien Species	N		P	P	P	P	P	P	P	P	P	P

NOTES:
Stag= staghorn coral;
Elk = elkhorn coral
Y = Yes
N = No
A = Present or threatened destruction, modification or curtailment of its habitat or range
B = Overutilization for commercial, recreational, scientific or educational purposes
C = Disease or predation
D = Inadequacy of existing regulatory mechanisms
E = Other natural or manmade factors affecting its continued existence
0-2 = Low
3 = Medium
4-5 = High
5+ = High and main cause of initial decline
SBU = Threat is believed to be significant, but ranking is UNKNOWN relative to other threats
P = potential threat, not known to be a threat at the current time, but could plausibly become a threat
* Range-wide, this threat is ranked as 2, but in U.S. jurisdictions, it is ranked as 3 overall

Disease

Threat Ranking:	5+
Impedes Recovery:	Y
Listing Factor:	C

Coral "disease" refers to not only clearly visible signs of infection by a pathogen or tissue loss, but also non-infectious physiological responses to abiotic (anthropogenic or environmental) stressors. One comprehensive definition states that disease is:

> *any impairment that interferes with or modifies the performance of normal functions, including responses to environmental factors such as nutrition, toxicants, and climate; infectious agents; inherent or congenital defects, or combinations of these factors* (Wobeser 1981).

Disease exists on a continuum from sub-lethal effects to morbid conditions leading to imminent death. Risk factors to coral health encompass biological, physical, and chemical agents or conditions. These are known to include microbial pathogens (bacteria and fungi), temperature extremes (warm and cold), and certain pollutants (e.g., heavy metals, oil constituents, antifoulants, pesticides) and likely include climate change, environment degradation, other toxicants, and physical damage. In few cases does the one-agent one-disease scenario exist, and even in those cases, features of the host, agent, and the environment can modulate whether overt disease occurs. Most often, the occurrence of disease is dictated by many inter-related factors and is best illustrated as a "web of causation" (see Figure 9)(Wobeser 1994). In this model any single factor may be necessary, but by itself, not sufficient to produce disease. Thus, to determine causation, a more holistic view must be adopted that includes the host (the coral animal, algal symbiont, and microbiota, i.e., the holobiont), the disease agent(s), and the environmental conditions.

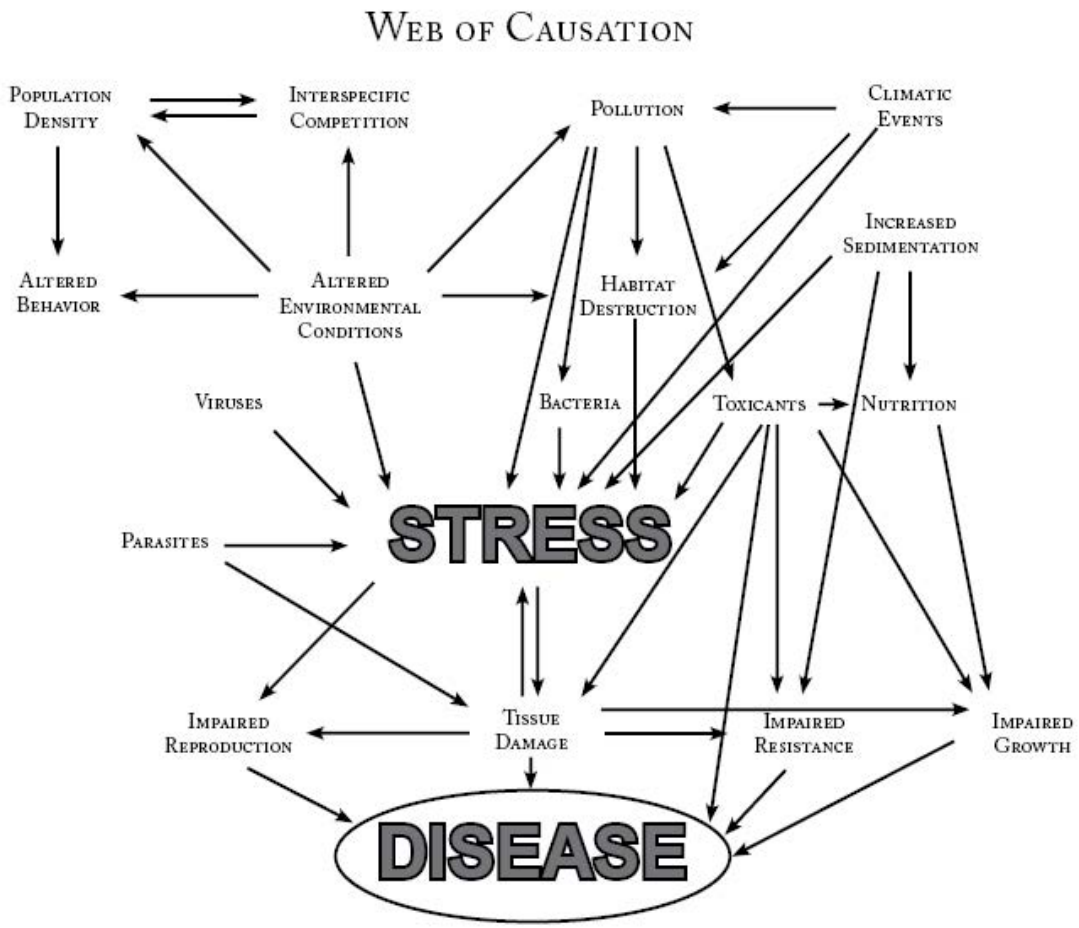

Figure 9. Web of Causation. Diagram provides an example to illustrate possible interactions and causal pathways that may result in a disease state (after Wobeser 1994).

Coral diseases have severely affected Atlantic/Caribbean coral reefs in general and particularly elkhorn and staghorn coral populations. Evidence demonstrates an increase in marine diseases, including coral diseases, during the past two to three decades (Harvell et al. 1999). Diseases are believed to be the primary cause of the region-wide decline of these two coral species beginning in the late 1970s. White band disease (WBD) is generally associated with the majority of disease-related mortalities in both staghorn and elkhorn corals (Aronson and Precht 2001). However, as with most coral diseases, the inconsistent phenomenological description of disease mortality patterns in elkhorn and staghorn corals and the lack of identification of a specific pathogen have greatly hindered the ecological as well as epidemiological understanding of WBD impacts and, more importantly, control of WBD. A second disease, termed white pox (WPx) or acroporid serratiosis (APS) (Sutherland et al. 2011), has been described as having devastating impacts on elkhorn coral, and a specific pathogen *(Serratia marcescens)* has been identified as the causal agent (Patterson et al. 2002, Sutherland et al. 2011) in corals in the Florida Keys. However, this agent has not consistently been found in elkhorn coral showing similar gross lesions in other geographic locations. Thus, there can be multiple etiologies for lesions that appear similar, rendering diagnosis of coral diseases from gross visual signs problematic.

White Band Disease (WBD)

WBD (Figure 10) was originally described in elkhorn coral as "a sharp line of advance where the distally located zooxanthella-bearing coral tissue is cleanly and completely removed from the skeleton, leaving a sharp white zone about 1 cm [0.4 in] wide that grades proximally into algal successional stages" (Gladfelter 1982). Specific literature descriptions of the pattern, rate, and progression of WBD in staghorn coral are rare, but usually describe a white band of skeleton occurring in the middle or at the base of live branches (Peters et al. 1983, Santavy and Peters 1997). Aronson and Precht (2001) suggest that WBD has had greater impact on staghorn coral than elkhorn coral population decline. The etiology of WBD has not been determined, although histological studies indicate that it is often associated with distinctive bacterial aggregates present in the calicoblastic epidermis (Peters 1984, Peters et al. 1997). Kline and Vollmer (2011), investigating the cause of White Band Type I, provided evidence that disease signs could be reproduced in apparently healthy staghorn corals by applying homogenates prepared from active WBD tissue or a 0.45 µm filtrate, but significantly less disease occurred with application of a 0.22 µm filtrate. Further disease infectivity was suppressed with Ampicillin treatment but not Tetracycline. Taken together these data suggest involvement of one or more bacterial agents in WBD Type I and that Rickettsiales bacteria previously suggested to play a role (Casas et al. 2004) is unlikely involved in this disease since Ampicillin is not effective against this agent.

Ritchie and Smith (1995, 1998) described a disease in staghorn coral as having a margin of bleached tissue between the denuded clean skeleton band and apparently healthy tissue (Ritchie and Smith 1995). This condition was subsequently termed WBD Type II (Ritchie and Smith 1998) and was linked with a bacterial infection by *Vibrio carchariae* (also referred to as *Vibrio charchariae* and *Vibrio harveyi*) (Gil-Agudelo et al. 2006).

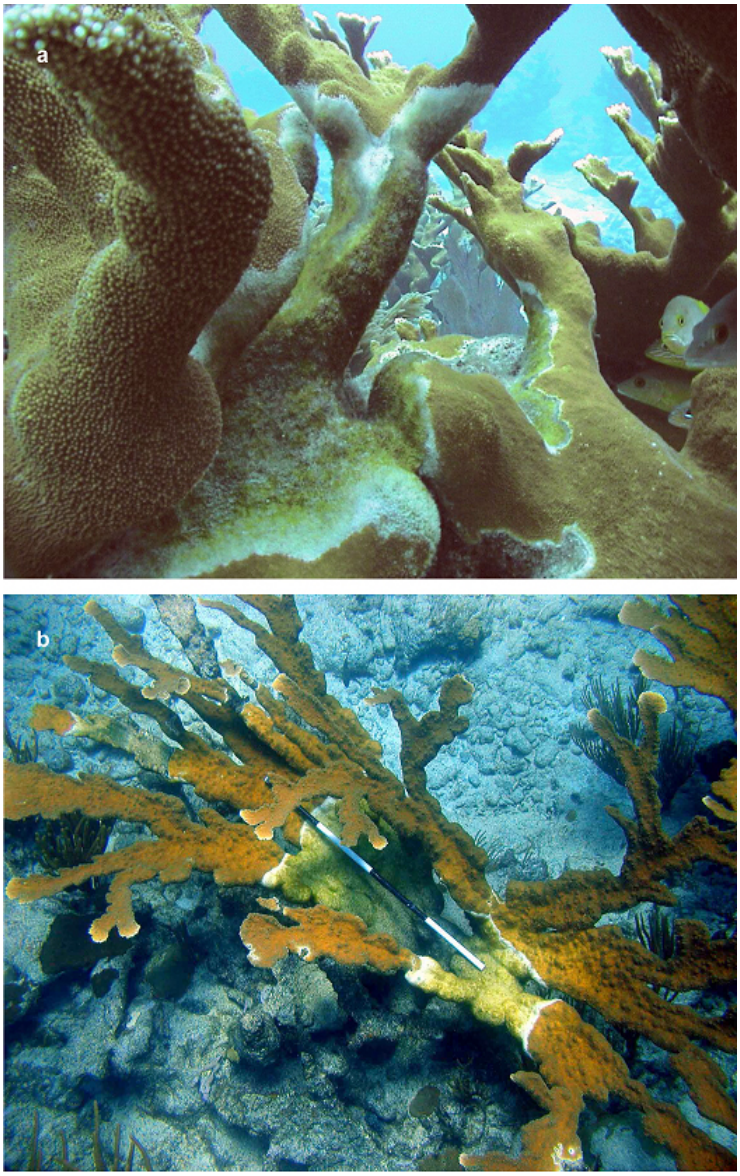

Figure 10. WBD on elkhorn coral in (a) the Florida Keys, and (b) Buck Island, USVI. Photo credit: (a) M. Miller; (b) P. Mayor.

White Pox (WPx)

The other major disease pattern affecting elkhorn coral is known by the name white pox (WPx) or acroporid serratiosis (APS) (Figure 11 and 12a), which manifests as multifocal, irregularly shaped, white lesions devoid of tissue. Although WPx has been described as a "new" disease (Patterson et al. 2002, Sutherland et al. 2011), there are early descriptions in the literature that are consistent with WPx. Other researchers have used the more general term "patchy necrosis" to refer to irregular denuded skeleton lesions affecting elkhorn coral (e.g., Bruckner and Bruckner 1997; Rodriguez-Martinez et al. 2001). Bak and Criens (1982) described an outbreak of "virulent" disease on elkhorn coral (and staghorn coral) that resembled WPx (i.e., "white spots (clean skeletal surface) on the coral branches [that] are enlarged through necrosis of the surrounding edge of living coral tissue [with] no discoloration at the living coral edge and within two weeks, the damage reached a maximum number of about 50 dead spots per (9 m^2)

quadrat" (Bak and Criens 1982)). Rogers et al. (2005) also documented WPx-like lesions on elkhorn coral from Buck Island, USVI in 1970.

A bacterial pathogen, *Serratia marcescens*, was originally demonstrated to cause WPx in Key West, Florida (Patterson et al. 2002) and later isolated from locations throughout the Florida Keys (Sutherland et al. 2011). On the other hand, limited surveys in the USVI did not identify *S. marcescens* in *Acropora* samples displaying lesions similar to those described for WPx (Polson et al. 2009). Subsequent source tracking work has traced pathogenic strains of *S. marcescens* to human sewage and potential vectors/reservoirs such as corallivores (Sutherland et al. 2011) in the Florida Keys. Lesions from this bacterial pathogen range in area from a few square centimeters to greater than 80 cm^2 (31 in^2) and can develop simultaneously on all surfaces of the coral colony (Patterson et al. 2002). Significant mortality of elkhorn coral (over 70 percent of living cover killed in certain sites) in the Florida Keys during the late 1990s has been attributed to WPx (Patterson et al. 2002). However, these disease observations occurred during and after a major bleaching event, and reliance solely on observations of gross lesions for identification of a specific disease is problematic. Irregular white lesions on elkhorn coral can only be ascribed to *Serratia marcescens* when its presence is confirmed by laboratory tests.

Although most of the 1970s to 1990s decline in elkhorn and staghorn coral abundance is attributed to WBD, the incidence of WPx appears to be increasing. Most monitoring information after 2000 indicates that lesion patterns resembling WPx (Figure 12) have higher prevalence in elkhorn coral than patterns resembling WBD. In elkhorn coral, the prevalence of WPx can vary substantially even over a small geographic area (Rogers et al. 2008, Weil et al. 2002). The first reported epizootic of patchy necrosis along the southwest coast of Puerto Rico was in December 1996 (Bruckner and Bruckner 1997), and yearly outbreaks have been observed since 2000. While 35 to 74 percent of the colonies on six reefs were affected by an outbreak in 2000, many of the colonies recovered completely (Bruckner 2002).

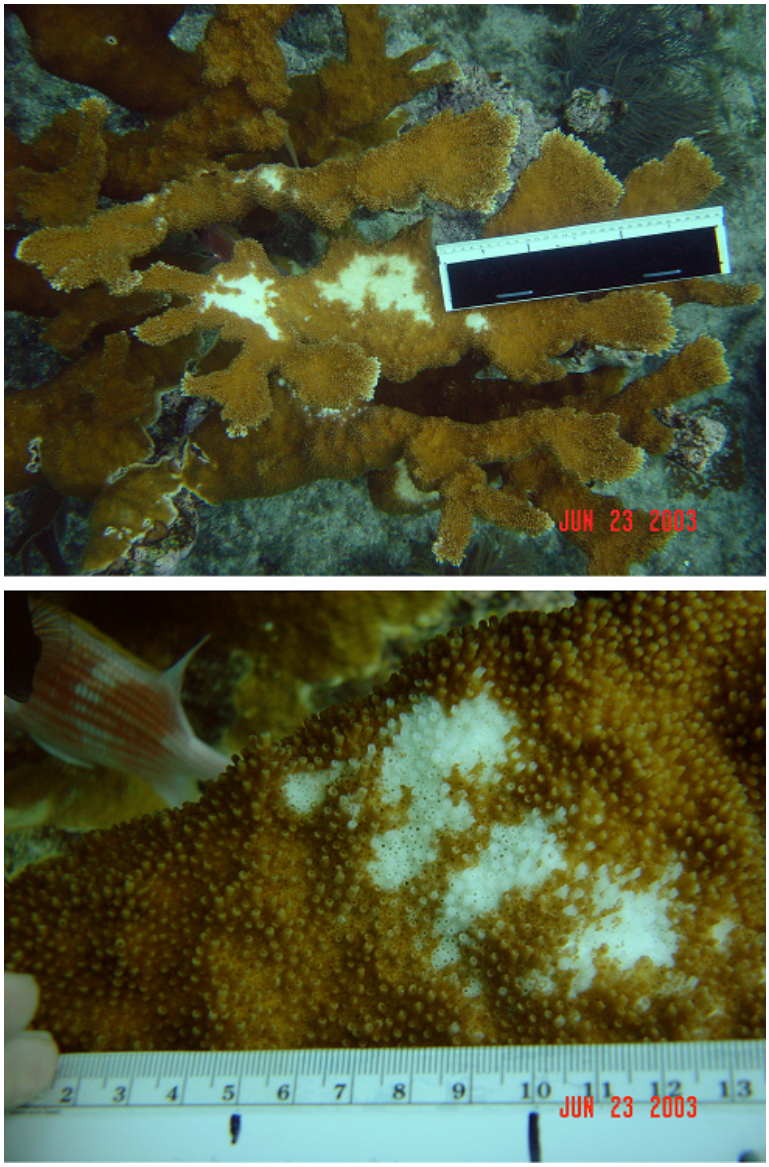

Figure 11. Two examples of "patchy necrosis" lesions on elkhorn coral in the Florida Keys. Such lesions may or may not constitute White Pox disease caused by *Serratia marcescens*. Photo credit: M. Miller.

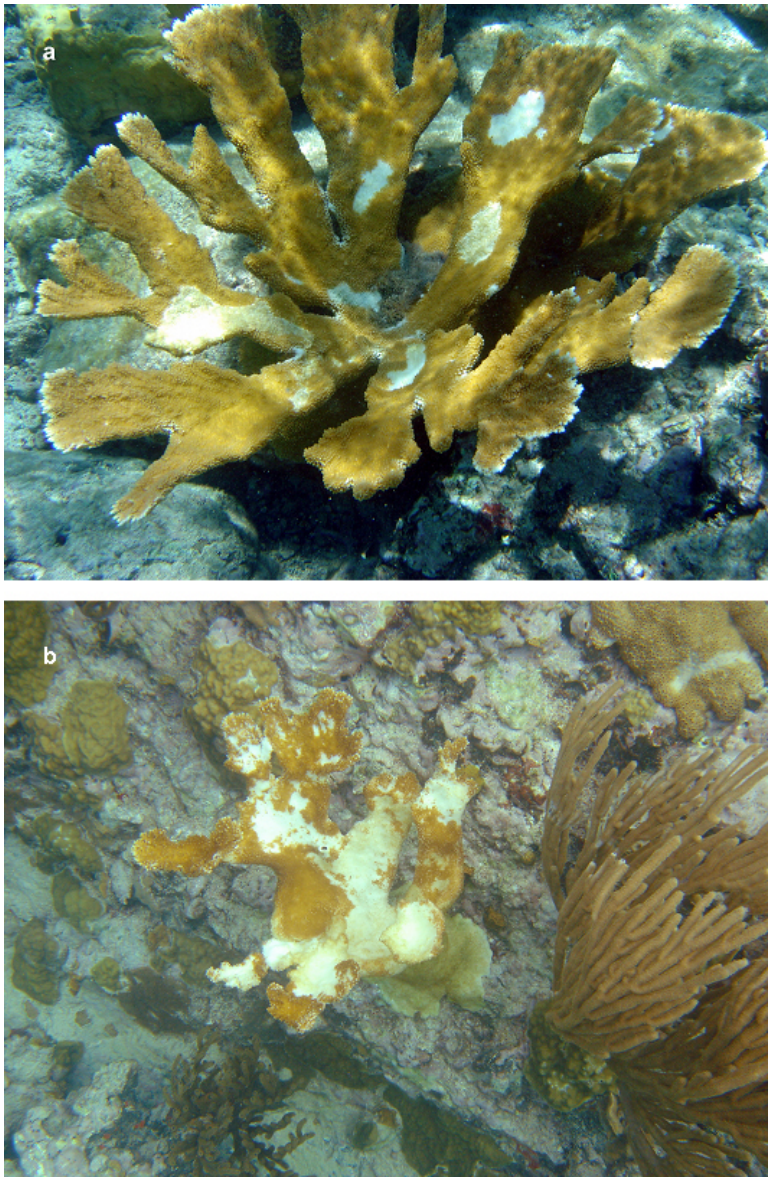

Figure 12. Examples of two diseases [WPx (a) and unidentified (b)] on elkhorn coral, St. John, USVI. Photo credit: C. Rogers.

Growth Anomalies and Other Diseases

Growth anomalies, characterized by protuberant whitened masses of tissue and skeleton that overgrow normal polyps, have been observed on elkhorn coral colonies and to a much lesser extent in staghorn coral in the Caribbean (Peters et al. 1986). These anomalies result in slow tissue loss, reduced branch extension, and loss of reproductive potential, but overall have minimal impacts at the population level relative to other diseases seen in elkhorn and staghorn corals. Although not yet described in elkhorn or staghorn coral, necrosis and infiltration by endolithic fungi, sponges, or small crustaceans have also been observed in *Acropora* spp. from Oman (Coles and Seapy 1998) and American Samoa (Work et al. 2008).

In addition to growth anomalies, there are numerous diseases with no known causative agent that afflict elkhorn and staghorn corals, many of which appear to be enhanced by high water temperatures and coral bleaching (Muller et al. 2007). Croquer et al. (2006) recently reported a ciliate disease affecting

elkhorn and staghorn corals, similar to a disease prevalent in Pacific *Acropora* spp. on the Great Barrier Reef. Williams and Miller (2005) described an outbreak of a transmissible disease that caused rapid tissue loss on staghorn coral in the Florida Keys in 2003. Progression rates ranged from 2 to 43 cm^2 per day with an average of 13 ± 11 (standard deviation) cm^2 per day, which translates to an average linear rate of 4 cm per day along a typical branch. The disease manifested as irregular, multifocal tissue lesions with apparently healthy tissue remaining in between, a description similar to elkhorn coral afflicted with WPx.

Disease Impacts

Diseases continue to have a devastating impact on existing elkhorn and staghorn coral populations. For example, an outbreak throughout the Florida Keys in 2003 affected 72 percent of tagged colonies of staghorn coral (N = 20) involved in a recovery monitoring project, with 28 percent of these suffering complete mortality and many more colonies ending up as tiny remnants of live tissue (less than 10 percent of colony alive) (Williams and Miller 2005). Mean rates of colony tissue loss were variable, but generally very rapid, averaging approximately 13 cm^2 (2.0 in^2) of tissue per day, but ranging up to 42 cm^2 (6.5 in^2) per day (Williams and Miller 2005). During this same time period, a fused-staghorn coral patch in Dry Tortugas National Park also suffered a disease outbreak, but prevalence and mortality were not quantified. In contrast, ongoing monitoring of extensive staghorn coral thickets to the north in Broward County, Florida, did not detect unusual levels of disease during this same period (B. Vargas-Angel pers. comm.). In other examples, massive rates of tissue loss including substantial whole-colony mortality in elkhorn coral were documented in 2005 following hurricane impacts in the Florida Keys (Williams et al. 2008) and following bleaching in the USVI (Muller et al. 2008).

Disease status/prevalence is available from various targeted monitoring programs. Of 60 elkhorn colonies in Hawksnest Bay, St. John, USVI that were monitored on a monthly basis from May 2004 through December 2006, 87 percent showed partial mortality due to disease, with WPx representing approximately 80 percent of these disease incidences (Muller et al. 2008). In Haulover Bay, St. John, USVI, 90 percent of 69 elkhorn colonies monitored monthly from 2003 to 2009 exhibited disease with more colonies infected with WPx (86 percent) than WBD (13 percent) (Rogers and Muller 2012). Targeted monitoring of tagged elkhorn colonies at five reefs in the upper Florida Keys from 2004 to 2010 showed a long term average of ~ 18 percent prevalence (i.e. percent of colonies affected by recent disease mortality), but approximately 30 percent of the overall observed tissue loss over this time frame is attributed to disease, greater than any other source (Williams and Miller 2012). No similar estimates are available from targeted monitoring of staghorn coral in these areas (USVI and Florida Keys).

In the Florida Keys from 1999 through 2001, elkhorn and staghorn corals were sampled for disease prevalence during synoptic surveys of 204 sites representing a range of hard-bottom and coral reef habitats (Swanson et al. unpublished data). Approximately 7.7 percent (± 5.9 percent standard error (SE)) of elkhorn coral sampled from northern Key Largo to south of Key West were recorded as having dead areas of exposed white skeleton of unknown cause(s), while another 5.5 percent (± 5.5 percent SE) were documented with WBD. Over the same study area, 0.4 percent (± 0.4 percent SE) of staghorn coral colonies was recorded as having lesions of unknown cause(s), and none were noted with active WBD conditions. Surveys in the Florida Keys of 235 sites during June to August 2007 indicated no staghorn or elkhorn colonies with active signs of disease (Miller et al. 2008b).

The Atlantic and Gulf Rapid Reef Assessment (AGRRA) surveys, conducted from 1997 to 2000, provide a valuable regional overview. However, the data on diseases in elkhorn and staghorn corals must be viewed with some caution because of the difficulty of identifying different diseases in the field and the varying expertise and experience of the observers (Lang 2003). For example, some observers noted

disease but did not distinguish between patchy necrosis and WBD. While the AGRRA program is extensive in geographic scope, it is limited in temporal scope, culminating in individual one-time surveys over a range of sites over several years (i.e., the surveys at different sites are from different years and seasons). Thus, it is not known if an individual AGRRA survey represents a common "baseline" condition or an outbreak.

In the 1997-2000 AGRRA surveys, the most frequently observed disease condition in elkhorn coral was patchy necrosis while WBD (the only recognized staghorn disease) was more prevalent in staghorn coral. Over 4 percent of elkhorn coral colonies were affected by disease with higher disease prevalence in the Netherlands Antilles (north) (18 percent), Bahamas (12 percent), Cayman Islands (7 percent), and Turks and Caicos (6 percent). Five areas had no signs of disease on elkhorn coral, specifically Costa Rica, Netherlands Antilles (south), Panama, USVI, and Venezuela. At least 6 percent of staghorn coral colonies were diseased, with greater prevalence documented from the Turks and Caicos (21 percent) and Cayman Islands (20 percent), while USVI (13 percent), Cuba (8 percent), and Bahamas (6 percent) had higher than average levels. Areas where no disease was recorded on staghorn coral were Jamaica, Mexico, Netherlands Antilles, Panama, and Venezuela. Low to moderate disease prevalence was documented along most of Cuba's south coast, but 38 percent of the *Acropora* spp. at one site was affected. Recent mortality was higher during 1998 and part of 1999 and was attributed to temperature stress during the 1998-99 El Niño-La Niña events. While overall (i.e., Caribbean and Western Atlantic-wide) disease prevalence of 4 to 6 percent as indicated by the AGRRA data may not appear to constitute a significant threat, it should be noted that this is an instantaneous measure. Thus, it gives no indication of the rapidity with which mortality might result or of the significance that this level of disease prevalence could have if a different colony is affected each year.

Causes of Disease

Although coral disease (specifically gross lesions or tissue loss) has been correlated with temperature, LBSP, and predisposition or heightened susceptibility following bleaching and infectious agents, little is really known about the root cause(s) of most coral diseases. In fact, there are few diagnostic criteria available to distinguish among the gross and morphological lesions described to date. Only recently have investigations begun to reveal possible mechanisms involved in the various pathological conditions found in corals. The temporal coincidence (decadal scale) associating increased disease impacts with increasing anthropogenic pressures to reef systems suggests that a link must exist, though WBD has devastated *Acropora* spp. populations both near and far from intense human habitation (e.g., Curran et al. 1994).

The discovery of *Serratia marcescens* as a causal agent of WPx suggested an anthropogenic source, as certain strains of this bacterium are human enteric residents that can be transported to the reef via human sewage and other LBSP. Though there are myriad possible sources of this bacterium (i.e., it can occupy a variety of animal guts), Krediet et al. (2009) recently showed that the WPx agent (PL100) is of human sewage origin. Subsequent studies in the upper and lower Florida Keys identified a unique strain of *S. marcescens* (PDR60) from human wastewater, the water column, the corallivorous snail (*Coralliophila abbreviata)*, non-acroporid corals, and white pox-affected elkhorn coral (Sutherland et al. 2010). Through lab experiments, they showed infection of *A. palmata* colonies with this strain of *S. marcescens* (PDR60), further indicting potential sources, reservoirs, and vectors. Other field microbiological source tracking work in the Florida Keys has not found *Serratia* associated with putative WPx lesions (Muller et al. 2008) or in local sewage sources (Lipp et al. pers. comm.). These findings point to the fact that coral diseases cannot be diagnosed in the field from gross visual signs and that

there can be multiple etiologies for gross lesions that appear similar. In addition, distinct strains of pathogens with varying levels of virulence may exist (Sutherland et al. 2011).

Several authors have suggested there is a link between increased incidence and/or virulence of coral disease with increased temperature (Harvell et al. 1999, Patterson et al. 2002, Bruno et al. 2007) that may be acting on the host susceptibility, agent virulence, or exacerbating local conditions. Although this phenomenon has been documented in other wildlife diseases, direct evidence of these mechanisms in coral is still unknown and is an important area of research. Increased numbers of elkhorn coral colonies with WPx (acroporid serratiosis) lesions and the number of lesions per colony have been observed in September and October when sea surface temperatures are greatest (Patterson et al. 2002). Muller et al. (2008) showed that increased disease impacts in elkhorn colonies were related to bleaching, though not to high temperature exposure *per se*. Ritchie (2006) also showed that the natural anti-microbial activity of elkhorn coral mucous was impaired during temperature-induced bleaching, suggesting greater susceptibility to infective agents. However, similar lesions have also been reported in March/April on elkhorn and staghorn corals when water temperatures are low (Williams pers. comm.), and staghorn disease outbreaks have been repeatedly observed during spring in the absence of warm temperature stress (Williams and Miller 2005, Nedimyer pers. comm.).

Summary

Although the number and identity of specific disease conditions affecting elkhorn and staghorn corals and the causal factors involved are uncertain, several generalizations are evident. Disease has had, and continues to have, major ongoing impacts on population abundance and colony condition of both elkhorn and staghorn corals. Diseases affecting these species may prevent or delay their recovery in the wider Caribbean. Disease constitutes an ongoing, major threat about which specific mechanistic and predictive understanding is largely lacking, thus precluding effective control or management strategies.

The conditions described above are those traditionally associated with the term “coral disease;” however, sub-clinical conditions prior to the presentation of gross lesions are, nonetheless, debilitating to coral health. These chronic or sub-lethal (i.e., sub-clinical) conditions may manifest as reproductive impairment, increased susceptibility to infectious agents, lack of vigor, inability to mount defense against biological agents, or inability to detoxify toxicants. At a population level these effects may manifest as reduced reproductive output, reduced larval recruitment or survival, reduced fitness, and/or retarded growth. Knowledge of the biological parameters that can be used to define health status in corals is critical to being able to develop screening tools for determining “at risk” populations for early detection and intervention. Research in these areas is only beginning to define normal parameters and identify patterns of change in these parameters that characterize disease conditions (especially sub-clinical conditions). As we understand the mechanisms governing coral pathologies, how agents disrupt normal functions of the host, its symbiont, or microbiota, and how environmental change influences the host-agent(s) interactions, we will be better positioned to identify which risk factors are impeding recovery in given locations and employ the most effective management actions to alleviate the threats.

Coral disease remains a high threat to elkhorn and staghorn corals in the Atlantic/Caribbean. There has been no change in its threat ranking (5+) since publication of the 2006 final listing rule. The 2014 final rule maintaining these species’ threatened listing (NMFS 2014) identified disease as a high importance threat to which the two species are highly vulnerable and as a threat contributing to their status (see Table 1).

Temperature

Threat Ranking:	5
Impedes Recovery:	Y
Listing Factor:	A,E

Corals thrive in seawater temperatures between 25 and 29°C (Wells 1957, Stoddart 1969). The western Atlantic-Caribbean coral reefs reside in the tropical-subtropical climatic zones characterized as seasonably warm. During summer doldrums and El Niño-Southern Oscillation (ENSO) periods, seawater temperatures may become lethal to organisms, especially at low tide, in shallow basins with limited circulation, at or near midday. The months of July through September are the warmest of the year. Mean August and September seawater temperature ranged from 27.7 to 31.4°C from 1879 to 1899, (Florida reef lighthouse data, Vaughan 1918), and mean July and August monthly seawater temperature was 30 and 30.4°C, respectively, between 1988 and 2008 (Sombrero Key, Florida weather buoy , http://www.ndbc.noaa.gov/data/climatic/SMKF1.txt). Temperatures above the warmest mean temperatures can cause stress to corals, and although they may be able to survive at elevated temperatures for a short period of time, temperatures several degrees (3-4) above mean monthly maximum for several days or prolonged exposure (several weeks) to slight increases (1-2 degrees) above mean monthly maximums can cause bleaching and mortality. High temperature results in physiological stress responses that can result in bleaching due to explusion of zooxanthellae, gastrodermal detachment (Gates et al. 1992), or autophagy (Downs et al. 2009). The major damaging risk factor due to elevated temperature and light exposure is the generation of reactive oxygen species (Lesser 1997, Downs et al. 2002, Lesser and Farrell 2004). Nitric oxide (Trapido-Rosenthall et al. 2005, Perez and Weis 2006) has also been implicated in reacting with reactive oxygen species. Bleaching (zooxanthellae loss) can affect coral growth, maintenance, reproduction and survival. Mayer (1914) reported that the lethal temperature for elkhorn coral was between 34 and 35°C. Shinn (1966) reported that staghorn coral expelled zooxanthellae at or near 33°C. Decreased larval survival and settlement of elkhorn coral have been found at temperatures above 30°C (Randall and Szmant 2009).

Severe coral bleaching occurred at sites around the world in 1983, the late 1980s, 1995, 1998, 2005, and 2010 (Glynn 1990, Wilkinson 2000, Wilkinson and Soutar 2007, Eakin et al. 2010). Bleaching events have become more frequent and spatially more widespread, and the impacts have become more intense during the past quarter century (McWilliams et al. 2005). As bleaching mortality has increased in frequency, coral reefs in many areas have already reached a point beyond which they do not have sufficient time to recover between events (Stone et al. 1999). Elkhorn and staghorn corals displayed severe impacts in the 1998 (Florida Keys) and 2005 (USVI) bleaching events. This pattern of increasing frequency and intensity of bleaching impacts on coral reefs throughout the world is projected to continue (Hoegh-Guldberg 1999, Donner et al. 2005).

Global climate change includes rising global atmospheric air and sea temperatures. Shallow reef habitats are especially vulnerable because they are more exposed to temperature fluctuations. In 2007, the Intergovernmental Panel on Climate Change (IPCC) noted that evidence is now “unequivocal” that the earth’s atmosphere and oceans are warming and concluded that these changes are primarily due to human activities resulting in emissions of “greenhouse gases,” notably carbon dioxide (CO_2). More than half of the observed increase in global average surface temperature from 1951 to 2010 was likely due to human activities (IPCC 2013). Since preindustrial times, atmospheric CO_2 has increased by 35 percent (from the preindustrial level of 280 ppm to 385 ppm in 2008). The 1995-2005 average rate of atmospheric CO_2 increase (1.9 ppm/yr) was 36 percent faster than the average rate of increase over 1960-2005 (1.4 ppm/yr) (Carbon Dioxide Information Analysis Center (CDIAC) 2009; data available at http://cdiac.ornl.gov/oceans/doc.html). Global ocean temperature has risen by 0.74°C (1.3°F) during the 20th century. Under the worst-case scenario (RCP8.5), AR5 projections of greenhouse gas emissions

indicate atmospheric temperature will likely increase by 2.6°C to 4.8°C (4.7°F to 8.6°F) in the years 2081-2100, relative to 1986-2005 (IPCC 2013). While reducing CO_2 and other greenhouse gas emissions is vital to stabilize the climate in the long term, greenhouse gases already concentrated in the atmosphere will produce significant changes in the global climate now and throughout the next century. These changes already have negatively impacted shallow reef habitats, including elkhorn and staghorn corals, and are expected to affect corals and coral reef ecosystems globally over the coming century.

Although climate change impacts were not identified as the primary cause of the initial decline of these two species, elevated ocean temperature has clearly caused major mortality. Mass coral bleaching that occurred in the 1980s and 1990s was correlated with abnormally high sea temperatures. The most severe bleaching events during these two decades were associated with El Niño events and were superimposed on generally elevated background sea temperatures due to global warming (Hoegh-Guldberg 1999). There is evidence that anthropogenic-induced warming played a role in the high Caribbean temperatures during the major bleaching event in 2005 (Trenberth and Shea 2006, Donner et al. 2007, Eakin et al. 2010). Frequency of mass bleaching events is projected to increase in the future with projected anthropogenic warming (Hoegh-Guldberg 1999, Donner et al. 2009, van Hooidonk et al. 2013). Given the time lag between greenhouse gas emissions and the physical climatic response, further warming is committed from CO_2 concentration levels already in the atmosphere. Current projections of increases in ocean temperature, coupled with the numerous other stressors acting on these depleted species, will inhibit recovery. Thus, reducing atmospheric CO_2 levels is likely needed to support recovery of elkhorn and staghorn corals. Model simulations by Donner et al. (2009) suggest that atmospheric CO_2 concentrations may need to be stabilized below 370 ppm to avoid degradation of coral reef ecosystems. Veron et al. (2009), based on the recent history of frequent mass bleaching events and correlated climate conditions, advocated the importance of atmospheric CO_2 concentrations of less than 350 ppm for coral reef health, as mass bleaching events, often associated with El Niño, began when atmospheric CO_2 concentrations were approximately 340 ppm. Veron et al. (2009) also discussed the 1997/98 mass bleaching event, when atmospheric CO_2 concentrations were 350 ppm, as the beginning of a decline in coral reef health from which there has been no significant long-term recovery.

High temperatures and bleaching have been correlated with coral disease (Bruno et al. 2007, Muller et al. 2008, Brandt and McManus 2009). An increased prevalence of infectious disease outbreaks has been associated with thermal stress even at temperatures below those required to cause mass bleaching (Bruno et al 2007). In work on the 2005 Caribbean bleaching event, Muller et al. (2008) found that elkhorn colonies showed higher disease prevalence with high temperature exposure and colonies that had bleached suffered greater levels of disease mortality. A causal mechanism linking elevated temperature and disease has yet to be determined, but it is clear that elevated temperature can exacerbate the effects of disease on coral populations.

Elevated temperatures have had a negative impact on elkhorn and staghorn corals through bleaching events and the relationship with coral disease. These impacts are expected to continue as temperatures rise, thereby impeding recovery of these coral species. Elevated temperature was identified as a threat contributing to the status of elkhorn and staghorn corals in the final rule listing them as threatened (NMFS 2006). While temperature impacts were not the primary cause of these species' major declines, the highly certain threat of rising temperatures to listed corals is ranked high (5) for all regions within these species' ranges (see Table 1). The combination of rising temperature and ocean acidification (see Acidification, below), both resulting primarily from anthropogenic increases in atmospheric CO_2, are likely to have synergistic effects and are among the greatest threats to elkhorn and staghorn coral recovery.

Loss of Recruitment Habitat

Threat Ranking:	4
Impedes Recovery:	Y
Listing Factor:	A

Elkhorn and staghorn corals, like most corals, require hard, consolidated substrate (i.e., stable, dead coral skeleton or hardbottom) for their larvae to settle or fragments to reattach (see Section C2. Habitat Use and Section D. Critical Habitat). Throughout much of these species' ranges, the proximity of shallow, hardbottom habitat to developed coastlines increases the frequency and extent of habitat loss due to impacts from a wide range of human activities (Wilkinson 2004, Waddell 2005, Waddell and Clarke 2008). Exacerbating natural challenges to successful recruitment is the actual amount of habitat being lost through direct removal and modification, which is associated with coastal construction, infrastructure installation, port expansion, and vessel groundings (USFWS 2004, Collier et al. 2007). Coastal construction and development can result in excavation of hardbottom habitat. The maritime industry, particularly freighters and other large vessels, has been responsible for numerous vessel groundings that frequently involve habitat for elkhorn and staghorn corals. Fishing and recreational boating, in many areas, contribute to habitat damage from anchors and fishing gear.

The quality and amount of substrate available directly influences settlement success and fragment survivorship. Habitat loss through burial or overgrowth can limit or prevent both larval recruitment and fragment stabilization. Benthic algae can limit the availability of appropriate habitat for successful sexual and asexual reproduction through overgrowth, preemption of available space, and allelopathic (chemical) interactions (Birrell et al. 2005, 2008, Kuffner et al. 2006). The zoanthid *Palythoa caribaeorum* is common in many shallow reef environments and is an aggressive competitor than can overgrow most sessile reef invertebrates (Suchanek and Green 1981) and pre-empt space in areas that formerly supported stands of elkhorn coral. Sediment accumulation on suitable substrate impedes reproductive success by preempting available substrate and smothering coral recruits. The presence of turf algae and cyanobacteria, which trap sediment, can lead to greater accumulations of sediment as compared to bare substrate alone.

The reduced ability of stony corals to recruit to substrate covered by benthic algae is well known (Birrell et al. 2008,). Over recent decades, the colonization of dead coral skeleton surfaces by benthic algae (thick turfs as well as fleshy macroalgae) has led to increased space-occupation on many Atlantic/Caribbean coral reefs, which impedes the recruitment of new corals (Williams et al. 2001, Aronson and Precht 2006). Macroalgal dominance is also attributed to reduced grazing regimes due to human overexploitation of herbivorous fishes (Hughes 1994, Jackson et al. 2014) and to the regional mass mortality of the herbivorous long-spined sea urchin *(Diadema antillarum)* in 1983-84. The decline of long-spined urchin populations resulted in a dramatic decrease in herbivory and increase in algal cover on many Caribbean coral reefs and is considered one of the main factors contributing to the phase shift from coral dominated to algae dominated reefs (de Ruyter van Steveninck and Bak 1986, Carpenter 1990, Hughes 1994, Gardner et al. 2003).

Fishing is the most widespread exploitative activity on coral reefs and over-fishing poses significant threats to the biodiversity and condition of marine ecosystems (Jennings and Polunin 1996). Over-fishing can influence the assemblages of fish species by affecting their abundance, size, growth, and mortality, but it can also modify species interactions such as competition and predation by altering the structural complexity of these assemblages (Auster and Langton 1999). Over-fishing can result in ecological extinctions as low abundances of species prevent effective interactions with other species,

resulting in changes in structure and function of coastal ecosystems (Jackson et al. 2001). Over-fishing can cause increased vulnerability of ecological systems to other natural and human disturbances such as nutrient loading, disease, storms, and climate change (Hughes 1994, Jackson et al. 2001, 2014).

Under low grazing pressures, coral larvae, algae, and numerous other epibenthic organisms may settle, but most young, developing coral larvae are rapidly outcompeted for space and have high mortality levels (Sammarco 1985, Arnold and Steneck 2011). Competition between algae and corals is widespread on coral reefs and is largely mediated by herbivory (McCook et al. 2001). It has been demonstrated that increases in herbivory can significantly enhance substrate quality and larval recruitment of corals (Carpenter and Edmunds 2006, Mumby et al. 2007b). Parrotfish are important grazers of Caribbean reefs, especially in light of the massive die-off of the long-spined sea urchin *Diadema antillarum* in the early 1980s, and diminished parrotfish populations due to fishing may have a severe impact on coral reef systems (Mumby et al. 2006). A Caribbean ecosystem model predicts that reefs with high grazing levels from *Diadema* populations would be more resilient to stressors such as hurricanes and nutrification but that in the absence of *Diadema*, reduction of parrotfish populations from fishing pressure would result in reef degradation and reduced resilience (Mumby et al. 2006). The modeled effects of reduced parrotfish populations were even more pronounced when initial coral cover was low, indicating an even higher importance of grazers to coral recovery on reefs with low coral cover.

The persistence of macroalgae under reduced herbivore grazing regimes may also have indirect effects on coral recruitment by impairing calcareous coralline algae (CCA) growth. Some CCA species provide chemical cues for settlement and enhanced post-settlement survivorship of coral larvae including *Acropora* spp. (Harrington et al. 2004, Ritson-Williams et al. 2010). Most CCA are susceptible to fouling by fleshy algae, particularly when herbivores are absent (Steneck 1986). While some species of parrotfish can have a negative impact on corals because of consumption of coral tissue as part of their diet (Rotjan and Lewis 2006), Mumby (2009) concluded that the weight of evidence supports the net beneficial effect of parrotfish on coral reefs for their ability to reduce algal cover, thus facilitating coral recruitment.

In addition to reduced herbivory, habitat loss due to macroalgal overgrowth can be associated with nutrients from Land Based Sources of Pollution (LBSP) (Lapointe et al. 2005, but see Szmant 2002). Nutrients are added to coral reefs from both point sources (e.g. readily identifiable inputs where pollutants are discharged to receiving waters from a single source such as a pipe or drain) and non-point sources (inputs that occur over a wide area and are associated with particular land uses). Anthropogenic sources of nutrients include sewage, stormwater, and agricultural runoff, river and inlet discharge, and groundwater. Natural oceanographic sources like internal waves and upwelling also deliver nutrients to coral reefs. Coral reefs generally have been considered nutrient-limited systems, meaning that levels of accessible nitrogen and phosphorus limit the rates of macroalgae growth. When nutrient levels are raised in such a system, growth rates of fleshy macroalgae are expected to increase. Whether this increase in productivity translates into higher abundance of macroalgae on reefs depends on the level of herbivory removing that biomass (Szmant 2002).

Increased sediments often accompany nutrients and chemical contaminants from terrestrial runoff. Sources of sediment include coastal erosion, resuspension of bottom sediments, run-off following clearing of mangroves and deforestation of hillsides, beach nourishment, and nearshore dredging and disposal for coastal construction projects and for navigation purposes. Sediment deposition and accumulation affect the overall amount of suitable substrate available for larval settlement, recruitment, and fragment reattachment (Babcock and Davies 1991, Birrell et al. 2005); both sediment composition and deposition affect the survival of juvenile corals (Fabricius et al. 2003). Actions designed to compensate for adverse impacts of planned coastal construction and development projects are often

inappropriate or insufficient to compensate for lost ecosystem services (USFWS 2004). Loss of habitat resulting from such direct destruction reduces available substrate for larval recruitment. Habitat degradation from sediment deposition and other factors may disrupt cues for larval settlement, leading to limited or failed recruitment potential and increased larval mortality.

The category "Loss of Recruitment Habitat" encompasses the threat of "competition" identified in the final listing rule (NMFS 2006) as a threat contributing to the species' threatened status, and trophic effects from over-fishing as identified as a medium threat contributing to the species' status in the 2014 final rule maintaining the threatened status of elkhorn and staghorn corals (NMFS 2014). Overall, direct destruction and degradation in quality of benthic habitat, largely manifested as widespread occupation of reef substrates by macroalgae and sediment-binding turfs, are likely to greatly impede elkhorn and staghorn coral recovery. Pervasive changes in reef trophic structure (including reduced herbivory), widespread coral mortality that provides increased space for algal colonization, as well as increased nutrient loads from LBSP, contribute to increased benthic algal cover. The failure of stony corals, including elkhorn and staghorn corals, to recruit to substrates characterized by macroalgal dominance or sediment-binding turfs is also well known. With coastal population and development projections on the rise, this is a serious threat to coral reefs (FWC 2008). For elkhorn and staghorn corals in the Atlantic/Caribbean, where recruits are rare (Richmond and Hunter 1990), the continued loss of structural habitat combined with habitat degradation may prevent successful recovery of these species (Tougas and Porter 2002). Therefore, the threat posed to recovery of listed corals from "Loss of Recruitment Habitat" is ranked as high (4) across the region (see Table 1).

Inadequacy of Existing Regulatory Mechanisms

Threat Ranking:	**4**
Impedes Recovery:	**Y**
Listing Factor:	**D**

There are numerous regulations that directly and indirectly pertain to management of corals and the coral reef ecosystem. The Atlantic *Acropora* Status Review (BRT 2005) summarized regulatory mechanisms protecting corals. At the time of listing, it was deemed that existing regulations were not sufficient to manage the threats affecting these two coral species. In most cases, management actions were aimed at protecting coral or coral reefs in general and did not specifically mention *Acropora* spp.

There are a number of territorial, state, and local regulatory mechanisms that generally afford protection to corals and coral reefs. Florida statutes and rules protect all of the Scleractinian corals, including elkhorn and staghorn coral, from collection, commercial exploitation, and injury/destruction on the sea floor (FS 253.001, 253.04, Chapter 68B-2.008 and 68B-42.009). The Coral Reef Protection Act of 2009 (House Bill 1423) provides additional protection to coral reefs by authorizing penalties for destruction of reef resources and allowing for repair and mitigation of damage. The Clean Vessel Act of 1994 regulates sewage discharge of vessels in state waters, and Chapter 99-395, adopted as a Law of Florida in 1999, regulates discharge from waste water treatment plants. Monroe County Ordinance 029-1989 passed in 1989 regulates the sale of phosphate containing detergents in the Florida Keys in an effort to reduce the introduction of nutrients into local waters. Additionally, Florida has a comprehensive state regulatory program that regulates most land, including upland, wetland, and surface water alterations throughout the state. This regulatory program also includes a Federal-State Programmatic General Permit and implementation of a state-wide National Pollutant Discharge Elimination System (NPDES) program. Activities located on or using State-owned sovereign submerged lands also require applicable proprietary authorizations, including consent agreements, leases, and

easements. State park, aquatic preserve, and Outstanding Florida Waters designations may provide additional protection to *Acropora* spp. located within these boundaries.

In Puerto Rico several laws and regulations exist that may aid in the conservation of corals. The most pertinent statute is the 2000 Law for the Protection, Conservation, and Management of Coral Reefs in Puerto Rico (Law 147). This law explicitly mandates the conservation and management of coral reefs in order to protect their functions and values, and provides for the creation of zoned areas in order to mitigate impacts from human activities. Law 147 also directs the identification and mitigation of threats to coral reefs from degraded water quality due to pollution and additionally requires an Environmental Impact Statement (EIS) for projects or activities that can negatively affect coral reefs. Law 137 (2000) directs the designation of priority areas as marine reserves. There are currently 13 natural reserves located on all coasts and offshore islands in Puerto Rico that have coral reefs within their boundaries. This spatial distribution of protected areas provides an infrastructure for management measures to protect *Acropora* spp. populations.

The Virgin Islands Coastal Zone Management Act of 1978 (Virgin Islands Code, T. 12, Ch. 21, Section 906(b)(7)) and the Indigenous and Endangered Species Act of 1990 (Virgin Islands Law VIC, T. 12, Ch. 2, Section 103 (a)) prohibit the collection of corals in the USVI. In addition, Virgin Islands law (VIC, T. 12, Ch. 1, Section 97) provides for the establishment of wildlife or marine sanctuaries for the purpose of protecting wildlife, including corals. The National Park Service has created two national monuments (Virgin Islands Coral Reef National Monument and the Buck Island Reef National Monument) to designate thousands of acres as non-extractive zones. These national monuments afford total protection to organisms, including *Acropora* spp., within their boundaries and encompass 7 percent of the shelf around St. Croix, and 3 percent of the St. John/St. Thomas shelf. Most recently (2002) the Virgin Islands Legislature passed Bill 12 that approved the establishment of an additional large marine park on the eastern end of St. Croix (St. Croix East End Marine Park).

Relevant federal management actions have a long history and address a number of different types of potential impacts on and stresses to coral populations including collection, harvest, damage, destruction, dredge and fill, non-point source pollution, and coastal construction. Federal regulatory mechanisms that provide protection to coral reefs include: Executive Order 13089 Coral Reef Protection; the Outer Continental Shelf Lands Act of 1953; the Coral Reef Conservation Act of 2000; the Magnuson-Stevens Fishery Conservation and Management Act; the Coastal Zone Management Act of 1972; the Rivers and Harbors Act of 1899; the Clean Water Act of 1987; National Environmental Policy Act; National Marine Sanctuary Act of 1972; Florida Keys National Marine Sanctuary Act of 1990; National Parks, Monuments, Reserves, and Sanctuaries; and Fisheries Management Councils and Fisheries Management Plans.

Existing local, state, territorial, and federal regulatory mechanisms most beneficial to elkhorn and staghorn coral have focused on addressing collection, commercial exploitation, and physical impacts, including damage from fishing gear, anchoring, and vessel groundings. Habitat protection has largely been attempted through establishment of marine reserves, parks, or protected areas. While these designations can regulate user activities within the boundaries of the protected area that can negatively impact elkhorn and staghorn coral (e.g., fishing, anchoring), they generally do not provide protection from activities outside their boundaries (e.g., terrestrial activities) that can affect these coral species. Protected areas are often too small and piecemeal to provide sufficient protection (Pandolfi et al. 2005). The number of jurisdictions and agencies involved with regulating land-based activities that can impact

coral reefs, sometimes geographically far-removed from the activity, impedes protection and a unified approach. In addition, potential impacts from specific activities are often evaluated in the absence of knowledge of other activities that can act simultaneously to degrade the species and/or habitat over time. In the United States, at least 20 federal agencies are responsible for over 140 federal ocean-related statutes creating separate and often conflicting legal mandates for fisheries, aquaculture, shipping, oil and gas exploration/development, and mining. The problem of fragmented governance is growing, as new activities in the sea such as offshore aquaculture, wind farms, and liquefied natural gas (LNG) terminals are increasing the potential range and severity of conflicts across sectors. Many scientists suggest that area-based management holds the key to resolution of this problem (Crowder et al. 2006, Young et al. 2007). The development and implementation of marine spatial planning is likely the best tool to balance conservation and multiple uses for reefs and all ocean resources. In addition to marine spatial planning, regulations pertaining to land use practices need to be improved for areas affecting coastal ecosystems by establishing water quality standards (e.g., nutrients, turbidity, pollutants) specific to coral reefs. Designation of standards is hindered by the lack of knowledge of threshold tolerances of corals in general, and *Acropora* spp. in particular, to these inputs.

The listing of both elkhorn and staghorn coral as threatened under the ESA and the establishment of the 4(d) rule and critical habitat rule under the ESA have afforded protection specific to these two coral species. The 4(d) rule was issued to apply section 9 prohibitions on take of these species. The term "take" means to hurt, hunt, shoot, capture, trap, kill, collect, bother, harm, or pursue an ESA-listed species, or attempt any of these activities. Under section 7 of the ESA, all Federal agencies must ensure that any actions they authorize, fund, or carry out are not likely to jeopardize the continued existence of a listed species or destroy or adversely modify its designated critical habitat. Under section 10 of the ESA, when non-Federal entities such as states, counties, local governments, and private landowners wish to conduct an otherwise lawful activity that might incidentally, but not intentionally, take a listed species, an incidental take permit must first be obtained from NOAA Fisheries. The ESA, thus, improves the protection of these two species and their habitat within the jurisdictional boundaries of the U.S.

There is considerable variation in relevant regulatory mechanisms throughout the nations within the Caribbean region. While many Caribbean nations have enacted some sort of coral conservation or protection program/regulation, most proactive coral initiatives/efforts in the region are small-scale with, at best, localized effects. It is important to note that many of these efforts are not being implemented nation-wide. Because the ranges of these two species span the Caribbean and many of the current populations occur outside U.S. jurisdiction, current U.S. regulations and management actions only affect a portion of the species. In addition, because these two species have a planktonic larval stage, the replenishment of colonies is reliant on upstream sources of larvae from populations that may not be afforded the same level of protection as those within the legal boundaries of the U.S. Thus, international efforts to protect and preserve these two species will be needed for their recovery.

Notably, some of the greatest threats to elkhorn and staghorn corals (i.e., those with the highest ranking such as disease, temperature and natural abrasion and breakage from hurricanes) are not easily manageable as they are, in part, naturally occurring phenomena. However, their impacts are likely elevated due to the cumulative effects of threats to the species. In particular, these major threats are likely exacerbated by global climate change (e.g., warmer temperatures, increased hurricane intensity) which is occurring because of the release of greenhouse gases into the atmosphere. Though the initial decline of these two species has not been directly attributed to global climate change, its effects are

likely to intensify the major threats to the species and impede their recovery. Thus, more national and international efforts to reduce atmospheric carbon dioxide and curb global climate change are needed.

The final listing rule (NMFS 2006) identified inadequacy of regulatory mechanisms as a threat contributing to the threatened status of elkhorn and staghorn corals. Additionally, the 2014 final rule maintaining the threatened status of elkhorn and staghorn corals (NMFS 2014) identifies the inadequacy of existing regulations to control greenhouse gas emissions, and thus the high importance threats linked to climate change, as contributing to the status and risk of extinction of these two species. Because existing regulatory mechanisms are insufficient to provide appropriate threat abatement for elkhorn and staghorn corals, they are impeding recovery of these species. The threat posed by inadequacy of existing regulatory mechanisms is high (4) throughout the region (see Table 1) because several of the major threats affecting these species are amenable to regulation, albeit with difficulty. National and international efforts are needed to address global climate change while additional international protections are needed to protect populations of elkhorn and staghorn corals throughout their ranges. In addition, regional (area-based) management and development of water quality standards specific to coral reefs are needed to abate threats from activities that can impact these two species.

Natural Abrasion and Breakage of Species

Threat Ranking:	**4**
Impedes Recovery:	**Y**
Listing Factor:	**E**

This threat is discussed below in relation to its effects on the habitat of elkhorn and staghorn corals (see Natural Abrasion and Breakage of Habitat). Hurricanes and other storm events cause more physical damage to elkhorn and staghorn corals than anthropogenic physical impacts because they affect large geographic areas. In addition to breakage or colony removal, storms also mobilize sediments and debris, causing abrasion of tissues and enhanced exposure to any associated pathogens or contaminants.

Although hurricanes and other storms are a natural mechanism of disturbance to elkhorn and staghorn coral populations, and fragmentation due to physical disturbance is an important mode of reproduction, major storm events have been associated with population declines in these two coral species even prior to the onset of major losses in the early 1980s (Woodley et al. 1981, Rogers et al. 1982). Bleaching and tropical storm disturbances have caused successive losses of elkhorn and staghorn coral cover in the Florida Keys (Miller et al. 2002, Williams et al. 2008). Tropical storms can bring benefits to reefs if the storms pass far enough away to prevent damage, but close enough to cool waters and reduce bleaching risk (Manzello et al. 2007). Historically, tropical storms likely fostered propagation of elkhorn and staghorn coral thickets through fragmentation, but recent observations from periods of frequent hurricane impact in the Florida Keys document a lack of successful recruitment of fragments and a severe population decline (Williams et al. 2008).

The final listing rules (NMFS 2006, 2014) identified abrasion and breakage as a threat contributing to the threatened status of elkhorn and staghorn corals. Currently, there is consensus that we are entering a cyclical (decadal) period of greater storm activity (Curry 2008). In addition, climate change is expected to result in an increase of tropical storm intensity (Knutson et al. 2008). Meanwhile, it seems that some elkhorn and staghorn coral populations may be less resilient to storm damage than in the past. Under natural conditions, hurricane damage is one of many forms of disturbance that corals have experienced for millennia. However, other anthropogenic stresses to coral reef ecosystems (sedimentation,

nutrification, over fishing) have reduced the ability of coral reefs to recover from disturbance by reducing coral recruitment, growth, and fitness (Nystrom et al. 2000). Staghorn and elkhorn coral may be less able to capitalize on the potential opportunity for asexual reproduction due to high mortality of fragments and reduced colony density (and reef rugosity in general (Alvarez-Filip et al. 2009)), reducing the tendency for storm-generated fragments to be retained in suitable habitat (e.g., Williams et al. 2008). This threat is rated "high" (4) across all jurisdictions and throughout the ranges of these species and, left unabated, is likely to impede recovery of these species (see Table 1).

Acidification	Threat Ranking: 4 Impedes Recovery: Y Listing Factor: E

Ocean acidification is a term referring to changes in ocean carbonate chemistry, including a drop in the pH of ocean waters, that is occurring in response to the rise in the quantity of atmospheric CO_2 and the partial pressure of CO_2 (pCO_2) absorbed in oceanic waters (Caldeira and Wickett 2003). As pCO_2 rises, oceanic pH declines. Carbonate ions (CO_3^{2-}, HCO_3^-) are used by many marine organisms, including corals, to build calcium carbonate skeletons. For corals, the concentration of the carbonate ions in the ocean is measured as the aragonite saturation state. Decreasing pH and aragonite saturation state are expected to have a major impact on corals and other marine organisms this century (Fabry et al. 2008). Coral reefs need a saturation state of 4.0 or greater to thrive, and it is generally agreed that a saturation state below 3-3.25 will result in reduced calcification at rates insufficient to maintain net positive reef accretion, resulting in loss of reef structure (Guionette et al. 2003, Hoegh-Guldberg et al. 2007). Saturation state in the greater Caribbean, while temporally and spatially variable, declined at a rate of 0.012 ± 0.001 per year between 1996 and 2006 (Gledhill et al. 2008). A Caribbean open-ocean aragonite saturation state of 4.0 was correlated with an atmospheric CO_2 level stabilized at approximately 360 ppm (Simpson et al. 2009). The relationship between atmospheric CO_2 and aragonite saturation state indicates that a Caribbean open-ocean aragontite saturation state of less than 3.8 correlates with current atmospheric CO_2 levels (approximately 400 ppm), and that a saturation state of 3.0 correlates with an atmospheric CO_2 level of 530-570 ppm (Simpson et al. 2009). Evidence is mounting that ocean acidification may have direct impacts on coral populations, in addition to ecosystem effects related to net calcification and accretion of reef habitats.

Direct Impact on Corals

A variety of laboratory studies conducted on corals and coral reef organisms (Langdon and Atkinson 2005) (Figure 13) consistently show declines in the rate of coral calcification and growth with rising pCO_2, declining pH, and declining carbonate saturation state. Through laboratory experiments, Renegar and Riegl (2005) showed that increased pCO_2 slows the growth rate of *A. cervicornis*. Laboratory experiments have also shown that skeletal deposition and initiation of calcification in newly settled corals is reduced by declining aragonite saturation state (Cohen 2007, 2009, Albright et al. 2008). Recent field studies have shown a decline in linear extension rates in *Porites* spp. from the Great Barrier Reef and Thailand that may suggest acidification impacts (De'ath et al. 2009, Tanzil et al. 2009) over decadal time scales. Further, a retrospective field study has shown that *A. palmata* in Curaçao is growing significantly more slowly now than it did in the 1970s, and it was suggested that this may be due, in part, to declining aragonite saturation state (Bak et al. 2009). A study by Schneider and Erez (2006) found that declining saturation state causes a similar reduction in calcification in a Red Sea congener, *A. eurystoma*. They showed that *A. eurystoma* calcification has already declined by 20 percent since pre-industrial times and is likely to decline by 35 percent more with the doubling of atmospheric CO_2

expected by the mid-21st century. This is consistent with estimates for other branching corals (Langdon and Atkinson 2005) and with atmospheric CO_2 increases in the latest IPCC assessment (IPCC 2013). Coral growth rates will likely continue to slow with rising atmospheric CO_2. Recent work on Pacific *Acropora* spp. suggests that acidification may reduce the threshold at which bleaching occurs (Anthony et al. 2009); however, elkhorn and staghorn corals have yet to be subjected to similar acidification studies. In addition to effects on growth and calcification, recent laboratory experiments have shown that increased CO_2 also substantially impairs fertilization and settlement success in *Acropora palmata* (Albright et al. 2010).

While the long term response of elkhorn and staghorn corals to ocean acidification in combination with other environmental stresses will take time to assess, reduced calcification and slower growth will mean slower recovery from breakage, whether natural (hurricanes and storms) or human (breakage from vessel groundings, anchors, fishing gear, etc.), or mortality from a variety of disturbances. Slower growth also implies even higher rates of mortality for newly settled corals that are vulnerable to overgrowth competition, sediment smothering, and incidental predation until they reach a refuge at larger colony size. Reduced calcification and slower growth means more time to reach reproductive size and reduces sexual and asexual reproductive potential.

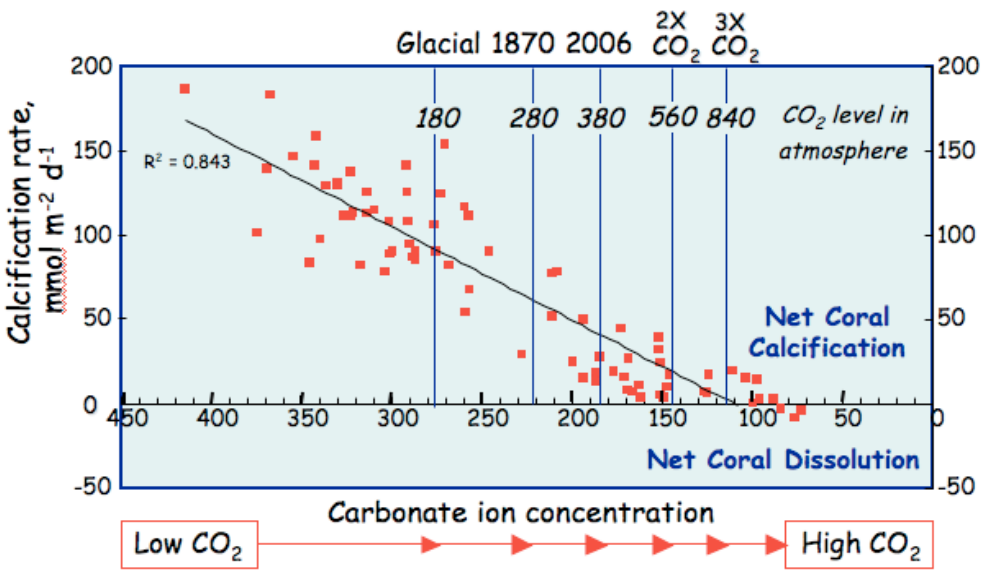

Figure 13. Effect of atmospheric CO_2 on calcification rate expressed as a percentage of the pre-industrial rate for a variety of corals and coral reefs from various studies (after Langdon and Atkinson 2005).

Acroporid Habitat Impacts

Many other important reef species will be significantly influenced by reduced seawater carbonate saturation state. Recent community mesocosm studies (Kuffner et al. 2008, Jokiel et al. 2008) showed dramatic declines in the growth rate of crustose coralline algae (CCA) and other reef organisms, and an increase in the growth of fleshy algae at CO_2 levels expected later this century. The decrease in CCA

growth, coupled with rapid growth of fleshy algae will result in less available habitat and more competition for settlement and recruitment of new coral colonies.

Recent modeling work has estimated the rates of grazing by herbivores that are required to maintain habitat conditions suitable for coral recruitment and the thresholds of coral cover combined with grazing rates predicted to facilitate the shift from an algal dominated to a coral dominated state (Mumby et al. 2007a). Expected increases in atmospheric CO_2 may require increased rates of herbivory to maintain conditions needed for successful coral recruitment due to reduced coral growth rates and a concomitant slowing of the rate of increase in coral cover that feed the model (Hoegh-Guldberg et al. 2007) (Figure 14). However, increased herbivore grazing is not completely substitutable for fundamental changes in coral recruitment and growth as a way to combat habitat changes associated with increased CO_2 and acidification. Additionally, there is evidence that rising atmospheric CO_2 and reduced carbonate saturation state may reduce the growth rate and recruitment of some urchin species (Havenhand et al. 2008, Stumpp et al. 2011). If long-spined sea urchins (*Diadema antillarum)* are similarly affected, ocean acidification could further deter the slow recovery of this important keystone species which declined dramatically during the 1983 mass mortality event in the Caribbean. Slower recovery of *D. antillarum* will perpetuate the current low grazing rates and higher algal competition for space, especially at sites where other herbivores such as parrotfishes have been overharvested.

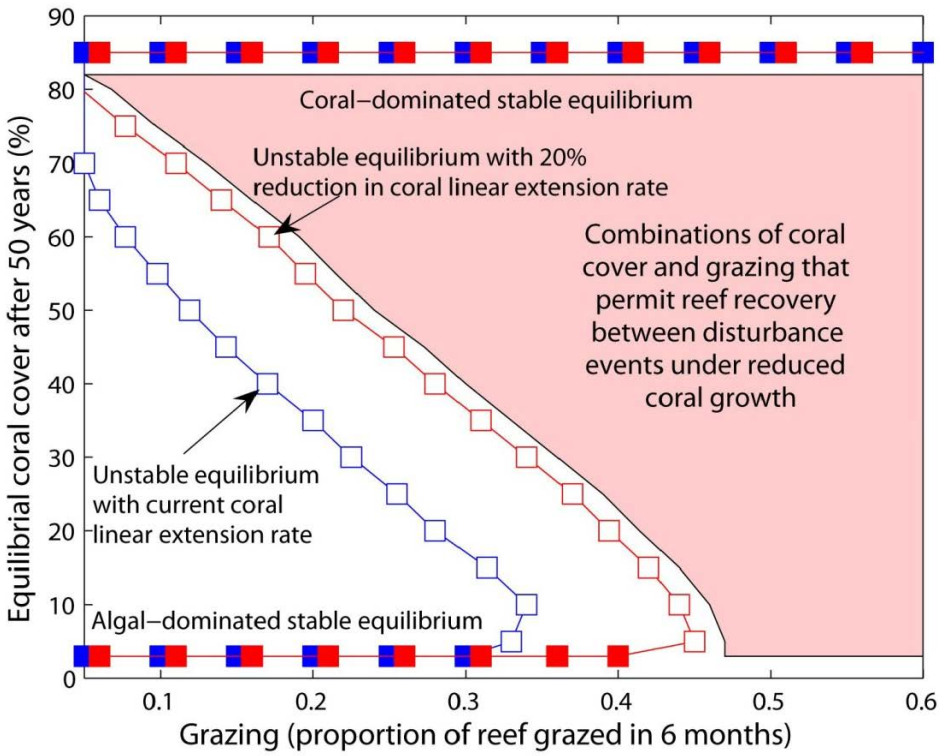

Figure 14. Reduction in the resilience of Caribbean forereefs as coral growth rate declines by 20 percent. Reef recovery is only feasible above or to the right of the unstable equilibria (open squares). The "zone of reef recovery" (pink) is therefore more restricted under reduced coral growth rate and reefs require higher levels of grazing to exhibit recovery trajectories (new analysis in Hoegh-Guldberg et al. 2007 using model from Mumby et al. 2007a).

The final documented impact of falling carbonate saturation state is a reduction of reef structural stability, which results from an increase in bioerosion and a decrease in secondary cementation. Low

saturation state of waters in the eastern Pacific Ocean has resulted in some of the highest rates of bioerosion seen globally and in poorly cemented, unstable, and fragile reef frameworks (Manzello et al. 2008). Low saturation state water not only slows growth rates of calcifying organisms, but decreases the rate of biochemical processes that create the cements that infill reefs. As atmospheric CO_2 rises, new reef formation in the Caribbean and elsewhere may be impeded and produce more fragile framework. This, in turn, would slow the accretion of stable reef structure (i.e., habitat of important reef-dwelling organisms such as herbivores) and make it more vulnerable to physical destruction.

Summary

The final listing rule identified elevated carbon dioxide as a threat that may be contributing to the threatened status of elkhorn and staghorn corals (NMFS 2006). Human activities contribute CO_2 into the atmosphere, and the amount of atmospheric CO_2 is increasing (IPCC 2013). Recent observations have shown that the current rate of increase of CO_2 emissions is exceeding the worst case scenarios used in modeling future climate change (IPCC 2007, IPCC 2013, Le Quéré et al. 2013). Considering the impact this will have on coral growth and calcification, ocean acidification resulting from rising atmospheric CO_2 represents a serious impediment to the recovery of elkhorn and staghorn corals. This is a global problem that will influence both listed species throughout their ranges. However, the severity of ocean acidification to corals has only become apparent within the last decade. There is still much knowledge needed to understand how this threat will impact particular species, including elkhorn and staghorn corals, and the reef ecosystem as a whole. While acidification was not the cause of the initial decline of these species, the severity of this threat to the growth, fertilization success, and recruitment of corals will make it more difficult for them to recover from the historically low populations currently present. The 2014 final rule maintaining these species' status as threatened (NMFS 2014) identifies ocean acidification as a high importance threat to which elkhorn and staghorn coral are highly susceptible and as a threat contributing to their status. Based on the current knowledge of the effects on coral growth and projections for the future, this threat is ranked as high (4) for all areas throughout the range of elkhorn and staghorn corals (see Table 1).

Depensatory Population Effects

Threat Ranking:	**3**
Impedes Recovery:	**Y**
Listing Factor:	**E**

It is well known from the field of conservation biology that when populations decline beyond a certain level, there are negative feedbacks that make recovery even more difficult (termed "depensation"). By definition, these processes do not initiate population declines, but they can accelerate declines and impede recovery. Examples include the so-called Allee effect (when organisms are rare enough that they cannot encounter appropriate mates) or genetic effects such as inbreeding depression (the increase in expression of deleterious traits when mating occurs between related individuals). Sexual reproduction in elkhorn and staghorn corals occurs by the spawning of eggs and sperm into the water column, so fertilization requires the haphazard encounter of gametes from different genetic individuals. Thus, as the density of elkhorn and staghorn coral colonies (and perhaps more severely, genotypes) has declined, dilution of gametes makes successful fertilization less likely. This Allee effect is surely impacting reproductive potential of elkhorn and staghorn coral populations, particularly in sites with low genotypic diversity (Baums et al. 2006). Contributing to Allee effect concerns for elkhorn coral are observations of spawning asynchrony. Observations at sites in the Florida Keys where distinct genotypes co-occur in close proximity indicate that they often spawn on different nights, precluding effective larval production (Miller et al. unpubl. obs.).

Genetic diversity (the variety of alleles present in a population and their distribution amongst individuals) is important in providing scope for populations to adapt to environmental changes. Reduced genetic diversity often results when species undergo a rapid decline such as elkhorn coral and staghorn coral have in recent decades. Reduced genetic diversity is more likely when population declines result from a potentially selective factor such as an infectious disease, in contrast to a non-selective factor such as hurricane damage (more likely to cause mortality independent of genotype). Thus, given the dominance of asexual reproduction and the rapid decline (largely from disease, a potentially selective factor) that have characterized elkhorn and staghorn coral populations, it is plausible that these populations have suffered a loss of genetic diversity that could compromise their ability to adapt to future changes in environmental conditions, at least in certain sectors of their ranges. However, there is no evidence that overall genetic diversity (expressed as heterozygosity) is lower than expected in most corals, including elkhorn coral (reviewed in Baums 2008).

Elkhorn and staghorn coral have been shown to retain moderate to high levels of genotypic diversity (i.e., the ratio of genetically distinct individuals to all colonies in a population or the relative abundance of genetic individuals) in many geographic areas (Baums et al. 2006, 2010, Vollmer and Palumbi 2007). However, low levels of genotypic diversity exist in some areas. For instance, elkhorn corals at many sites in the Florida Keys have a very low level of genotypic diversity (i.e., several robust thickets are constituted by a single genetic individual) indicating a high reliance on asexual reproduction to maintain populations (Baums et al. 2006). However, staghorn coral in Florida showed higher levels of diversity, indicating a more even reliance on sexual and asexual reproduction (Baums et al. 2010). Genetic studies have found that genetic exchange is restricted between populations separated by greater than 500 km, emphasizing the importance of locally diverse populations to recovery of these two species (Baums et al. 2006, 2010, Vollmer and Palumbi 2007).

The *Acropora* BRT (2005) ranked a threat category termed “loss of genetic diversity” as “low,” and the final rule listing elkhorn and staghorn coral as threatened (NMFS 2006) identified the threat of loss of genetic diversity as contributing to their status given their reduced population sizes. The ART decided to broaden this category (currently termed “Depensatory Population Effects”) to include the more certain Allee effects of reduced colony/genotype density. The 2014 final rule maintaining elkhorn and staghorn corals as threatened species (NMFS 2014) evaluated the species’ demographic features which are related to depensatory population effects. The final rule identifies depensatory population effects as contributing to these species’ status and risk of extinction. Hence, this threat category is given a higher threat ranking of medium (3) due to the likelihood that Allee effects are impairing larval production and thereby impeding these species’ recovery at current conditions. An exception is the elkhorn coral population in southeast Florida, where this threat is ranked as high (5) due to the extreme rarity of this species in this region (see Table 1).

Sedimentation

Threat Ranking:	**3**
Impedes Recovery:	**Y**
Listing Factor:	**A,E**

Sediments enter the reef environment through many processes that are natural or anthropogenic in origin, including erosion of coastline, resuspension of bottom sediments, and terrestrial run-off. Coastal development is a major cause of increased sedimentation, and heavy sedimentation is associated with lower coral species richness and abundance, lower growth rates, decreased calcification, decreased net productivity, and lower rates of coral recruitment (Rogers 1990, Dutra et al. 2006). Sedimentation rates can fluctuate, depending on the time of year (e.g., dry vs. wet season) and on daily changes in weather conditions. If sediments accumulate, they can smother living corals, resulting in bleaching or mortality.

Existing data suggest that coral reproduction and recruitment are far more sensitive to changes in water quality than adult corals (Fabricius 2005). Accumulation of sediments can inhibit larval settlement and smother coral recruits (Babcock and Davies 1991, Fabricius et al. 2003). Settlement rates for coral larvae, and reattachment rates for fragments, are near zero on sediment-covered surfaces, and sedimentation tolerance in coral recruits is at least one order of magnitude lower than for adult corals (Fabricius 2005). See also Loss of Recruitment Habitat.

Sediment may also enter the reef environment through nearshore dredging activities for coastal construction and navigation projects. The dredging process generally results in a sediment plume which may settle onto corals adjacent to or downstream from the dredged area. Whether and to what extent there will be impacts to corals located adjacent to dredging projects depends on several factors, including the type of dredge utilized, the type of sediments and the size of the area being dredged, the hydrodynamic conditions of the dredging site, and the duration of active dredging. Each of these factors influences the size, settlement time, and ultimate settling site of the sediment plume. Nieuwaal (2001) presented several examples showing that dredging can damage coral reefs.

Elkhorn and staghorn corals appear to be particularly sensitive to sediment deposition and shading effects from increased sediment regimes. Both species require relatively clear, well-circulated water and are highly dependent upon sunlight for nourishment (Porter 1976, Lewis 1977). Both elkhorn and staghorn corals have poor capacity to remove coarser sediments (250-2000 µm) and only slightly more capacity for removing finer sediments (62-250 µm) (Hubbard and Pocock 1972). Water movement (turbulence) and gravity are probably more important in removing sediments from these species than their capabilities of sloughing sediments in still water (Porter 1987).

Rogers (1983) investigated the effects of sedimentation on staghorn coral, elkhorn coral, *Diploria strigosa*, *D. clivosa*, and *Orbicella* (formerly *Montastraea*) *annularis*. Elkhorn coral was the least tolerant of sediment deposition, as single applications of 200 mg/cm^2 to colonies caused coral tissue death as sediments accumulated on the flattened (horizontal) portions of the colonies. The widely spaced, cylindrical branches of staghorn coral facilitated passive sediment removal, making this species more tolerant of sediment deposition. However, Hodel and Vargas-Ángel (2007) noted degenerative histopathological changes in staghorn coral exposed to sedimentation rates of 200 mg/cm^2, indicating sub-lethal damage to the coral and compromised health. In another experiment, Rogers (1979) shaded a 20 m^2 area of reef as a partial simulation of high sediment conditions and found that staghorn coral (the most abundant species in this area; 45 percent of the total living corals) was the first to respond to shading. Three weeks after shading was initiated, most colonies of staghorn coral were bleached. Shading was terminated after five weeks. After six weeks, the growth tips of the staghorn coral were deteriorating or had been grazed away. A few branches recovered; most were dead and covered with algae. After seven weeks, there were more algae on the branches and further disintegration of branch tips.

The final listing rule (NMFS 2006) identified sedimentation as a threat contributing to the threatened status of elkhorn and staghorn corals. Similarly, the final rule maintaining the two species as threatened (NMFS 2014) lists sedimentation as a threat contributing to their status because of their susceptibility to this threat. The steep island topography of Puerto Rico and the USVI increases the sediment loads in terrestrial run-off, which increases the exposure to sediment accumulation on the surrounding coral reefs. Thus, in these territories, the threat of sedimentation is ranked medium (3) for staghorn corals and high (4) for elkhorn corals due to their differing morphology. In the Florida Keys, sedimentation is ranked as a low (1.5) threat to both coral species because of the low topography and the distance of elkhorn and staghorn corals from land. In southeast Florida, sedimentation is ranked as a medium (3) threat for elkhorn and staghorn corals because they are more often subject to impacts from nearshore

coastal construction (e.g., channel dredging) and shoreline protection (e.g., beach nourishment) projects. Range-wide, the threat of sedimentation is ranked as medium (3), relative to other threats affecting elkhorn and staghorn corals in the wild. Left unabated, this threat is likely to impede recovery of elkhorn and staghorn corals.

Predation

Threat Ranking:	3
Impedes Recovery:	Y
Listing Factor:	C

There are numerous organisms that create lesions on the surface of scleractinian corals, including several predators (corallivores) and species that are predominantly herbivores (damselfish and parrotfish). While many corallivores are inconspicuous, there are several families of reef fishes (parrotfish, butterflyfish, filefish, pufferfish, triggerfish, and damselfish), prosobranch gastropods, annelid polychaetes, sea urchins, and various crustaceans that create prominent lesions on living surfaces of their prey (Glynn 1990). Only a few predators are known to create prominent lesions on elkhorn and staghorn corals, including gastropods *(Coralliophila abbreviata)*, fireworms *(Hermodice carunculata)*, damselfish *(Stegastes planifrons* and *Microspathodon chrysurus)*, and stoplight parrotfish *(Sparisoma viride).* All of these predators are generalists, feeding on a wide range of coral (and in some cases, algal) prey, but in some cases may create greater impacts on elkhorn and staghorn corals. For instance, *C. abbreviata*, while occurring on 20 scleractinian coral species, is concentrated on six species of corals and creates conspicuous feeding scars only on staghorn and elkhorn corals (Ott and Lewis 1972, Miller 1981, Hayes 1990, Bruckner et al. 1997, Baums et al. 2003b). Larger *C. abbreviata*, which are predominantly female, are most often associated with branching *Acropora* spp. where they can occur in aggregations of up to 20 or more (Baums et al. 2003b). On elkhorn coral they create prominent grazing scars that progressively increase in area and can kill entire colonies, sometimes from subsequent tissue loss after predation has ceased (Bruckner et al. 1997, Baums et al. 2003a); however, this is not common except on small colonies. Snails also are often associated with diseased corals and can transmit disease conditions between affected and apparently healthy staghorn coral (Williams and Miller 2005). Prevalence data from throughout the Caribbean indicate that approximately 10 to 20 percent of *Acropora* spp. colonies harbor snails (Baums et al. 2003a). The rate of consumption by *C. abbreviata* is highly variable, partially dependent on the size of individual gastropods and number of gastropods in each aggregate, and may reach 6.5 cm^2 (2.6 in^2) of coral tissue per snail per day (Bruckner et al. 1997). Average tissue loss rates are probably closer to 1.5 cm^2 (0.6 in^2) of coral tissue per snail per day (Baums et al. 2003b). Given the larger size of snails on *Acropora* spp. and the presence of large aggregations that are predominantly female, gastropods are likely to consume much more tissue than on other species of coral and produce exponentially higher numbers of larvae (Bruckner et al. 1997, Johnston and Miller 2007). Long term demographic monitoring in the Florida Keys has estimated snail feeding to account for 29 percent of overall elkhorn coral tissue loss between 2004 and 2010 (Williams and Miller 2012); it was the most prevalent condition and accounted for the third highest source of tissue loss after fragmentation from hurricane impact and disease (Williams and Miller 2012). Snail predation clearly represents a significant potential source of progressive tissue loss, and its effects are more pronounced in areas where *Acropora* abundance or colony sizes are reduced and predation pressure remains constant. However, these snails are rare or absent from *Acropora* spp. stands in certain areas (e.g., Bocas del Toro, Panama, Baums pers. comm.; Dry Tortugas, Miller pers. observ.; Bajo Gullardo, Puerto Rico, Bruckner pers. observ.).

Fireworms most commonly feed on the branch tips of staghorn coral and protuberances of elkhorn coral, creating conspicuous white lesions, although they often feed at night and may be missed during

surveys (Marsden 1962, Lizama and Blanquet 1975, Dustan 1977). Vargas-Ángel et al. (2003) observed high densities of fireworms (86-618 fireworms ha^{-1}) in staghorn coral thickets in southeast Florida, but predation scars affected less than 0.2 percent of the staghorn coral cover, suggesting they are of minor importance in these populations at this time. However, fireworm feeding scars can be spatially patchy, and they may exacerbate tissue loss from other causes.

Although these predators do not often kill entire colonies, there are several possible mechanisms of additional indirect impact. For example, fireworms preferentially prey on the growing tips (including the apical polyps) of staghorn coral, which may disproportionately reduce growth of the colony for prolonged periods of time. Additionally, corallivores are frequently, and perhaps disproportionately, found on colonies affected by disease, and have been shown to act as vectors for coral disease (Sussman et al. 2003, Williams and Miller 2005, Aeby and Santavy 2006). Generalist predators have also been reported to concentrate on remnant *Acropora* spp. populations following host coral decline (Knowlton et al. 1990, Baums et al. 2003a), impeding recovery. For example, after Hurricane Allen struck the north coast of Jamaica in 1980 and greatly reduced the populations of elkhorn and staghorn corals, *C. abbreviata* (and other predators) continued to feed on remnant staghorn coral colonies, further reducing population abundance and the potential for recovery (Knowlton et al. 1981, 1990). This is an example of another depensatory mechanism whereby generalist predators can impact prey populations disproportionately when they are rare. Recent experimental work in Hawaii has demonstrated that when coral density is low, corallivory occurs with greater frequency and can result in complete mortality of small colonies (Jayewardene et al. 2009).

The three-spot damselfish (*Stegastes planifrons*) establishes algal farms in the midst of healthy, growing coral by biting at and killing live tissue with subsequent colonization of these dead skeletal areas by filamentous algae. Because elkhorn and staghorn corals grow relatively quickly, tissue may regenerate over the lesions, although more frequently continued coral growth results in chimney-like structures that encircle the algae and prevent it from spreading to adjacent areas. Damselfish prefer staghorn and elkhorn corals but will establish territories around other species when these two coral species are rare (Thresher 1976, Brawley and Adey 1977, Kaufman 1977, Itzkowitz 1978, Williams 1978, Sammarco and Carleton 1982). Isolated small colonies of staghorn coral, however, typically have a high prevalence of damselfish occupation that can contribute to their demise (M. Miller pers. obs.).

Fish corallivores affecting elkhorn and staghorn corals include large initial phase and terminal phase stoplight parrotfish (*Sparisoma viridae*, which excavate skeleton) and yellowtail damselfish (*M. chrysurus*, which affect mainly surface tissue). Lesions from both these sources tend to heal quickly (Bruckner pers. observ.) and thus do not represent a significant threat. The long-spined sea urchin *(Diadema antillarum)* is known to feed upon live elkhorn and staghorn coral tissue (Bak and Eys 1975, Sammarco 1980), but impacts on standing colonies are likely to be minimal as they tend to feed on algae at the base of colonies. They also may graze coral recruits as they non-selectively remove algae from reef substrates.

The final listing rule (NMFS 2006) identifies predation as a threat contributing to the threatened status of elkhorn and staghorn coral. Similarly, the final rule (NMFS 2012) maintaining the two species as threatened lists predation as a threat contributing to the status of the species due to their susceptibility to this threat. Overall, corallivores can have important direct and indirect impacts on elkhorn coral and staghorn coral, and are likely to impede recovery of these coral species. Their impacts are greater in the current scenario of low coral abundance as their generalist habits (i.e., occupying a wide range of coral host species) have allowed them to persist at high abundances despite decreases in the abundance of acroporid prey. Therefore, the threat of predation is ranked as medium (3) for the region (see Table 1) with some geographic and species-specific variation due to differences in observed predation levels. In

the Florida Keys, the threat posed by predation is low (2) for staghorn coral and medium (3) for elkhorn. In southeast Florida (i.e., Palm Beach, Broward, and Miami-Dade Counties) this is a low-ranked threat (2) for both listed coral species. Predation is ranked as a high (4) threat to elkhorn coral in Puerto Rico and as a medium (3) threat to staghorn corals. In USVI, the threat to both elkhorn and staghorn corals is medium (3) (see Table 1).

Anthropogenic Abrasion and Breakage of Species

Threat Ranking:	**2-3**
Impedes Recovery:	**Y**
Listing Factor:	**E**

Like the threat of "Natural Abrasion and Breakage," this threat affects both the species and the habitat of elkhorn and staghorn corals (see Anthropogenic Abrasion and Breakage of Habitat). Human activity in coral reef areas is another source of abrasion and breakage of elkhorn and staghorn corals. These activities include boating (Figure 15), anchoring, fishing, recreational SCUBA diving and snorkeling, and an increasing variety of maritime construction and development activities. Physical impacts from divers, vessel groundings, anchors, and marine debris are threats to coral reefs and present a direct disturbance to the coral environment. The shallow habitat requirements of elkhorn coral, in particular, render it susceptible to damage from such activities.

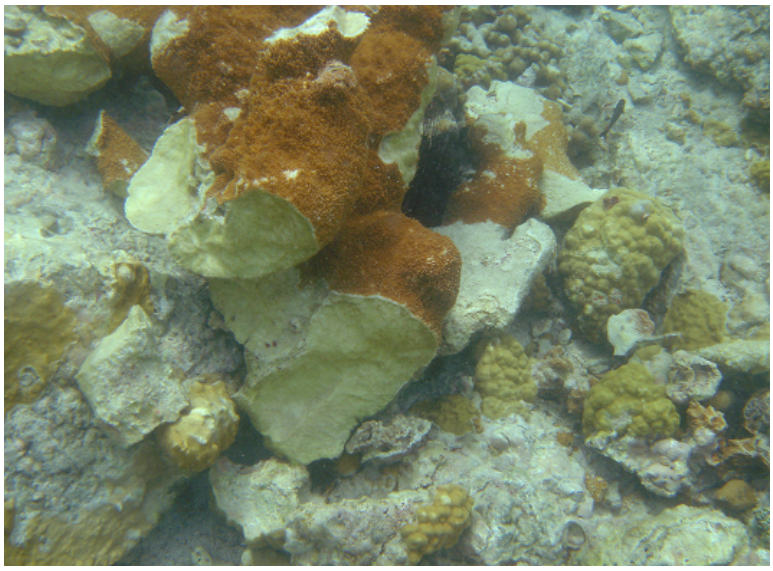

Figure 15. Boat damaged elkhorn coral, St. John, USVI. Photo credit: C. Rogers.

The aesthetic attractiveness of elkhorn and staghorn corals and associated species are engaging to recreational sightseers using either snorkel or SCUBA. While some of the interaction with these two coral species by recreational users is passive, elkhorn and staghorn coral are also subject to being kicked, stood upon, or touched, resulting in breakage. Divers with gloves were reported to have significantly higher numbers of interactions with all types of corals than divers without gloves, but weekly touching had no externally detectable level of impact to the corals (Talge 1991). A study from Grand Cayman has shown that sites with high visitation (greater than 6,000 visitors per year) had lower coral diversity and cover, particularly for massive coral species, compared to sites with lower visitation (fewer than 800 divers in a year) (Tratalos and Austin 2001). However, a study in the Florida Keys found that conservation briefings on dive boats significantly reduced the impacts of SCUBA divers on the reef

(Camp and Fraser 2012). The Florida Keys support 3.6-million person-days of snorkeling and SCUBA diving by residents and visitors per year (Johns et al. 2003). Based on these studies, this level of usage likely has an ecological impact on Florida Keys coral reefs including its remnant elkhorn and staghorn coral populations.

Vessel groundings

U.S. reefs in the Atlantic/Caribbean are annually impacted by 3-4 large ship groundings and hundreds of small boat groundings (Collier et al. 2007, Waddell and Clarke 2008, FDEP unpublished data, NOAA unpublished data). These impacts can cause fundamental changes to a reef's structural topography and biological communities by dislodging and fracturing corals, pulverizing coral skeletons into small debris-rubble, displacing sediment deposits, destabilizing bottom geology, flattening the topography, and destroying or fracturing the reef platform (See Anthropogenic Abrasion and Breakage of Habitat). Contact of the ship's hull with the bottom usually transfers toxic anti-fouling paint to the sea floor which can negatively affect recovery of the affected area (Negri et al. 2002). Salvage operations often result in additional damage due to inappropriate methods and poor control of operations. The *Fortuna Reefer* grounding at Mona Island, Puerto Rico in 1997 is a case where the use of sinking tow cables employed in salvage operations caused more extensive damage to elkhorn coral colonies than the original grounding incident itself. In some cases, the ship's hull is ruptured, and cargo and fuel are spilled on the reef.

The shallow habitat of elkhorn coral makes it especially vulnerable to vessel groundings, and there is evidence that certain populations near high boat traffic areas (particularly recreational boat traffic) are suffering chronic damage from repeated groundings (NOAA Restoration Center, unpublished data). Numerous groundings in south Florida, the Florida Keys, Puerto Rico and USVI have resulted in relatively significant localized impacts to elkhorn and staghorn corals. For example, the *Columbus Iselin* foundered in the spur and groove habitat at Looe Key Reef after its 1994 grounding. The grounding site was in an area where the coral community had been quantitatively studied (Wheaton and Jaap 1988). The wreck devastated organisms, including elkhorn and staghorn corals, where the ship came to rest, and because the ship was hard aground for several days, the pounding of the hull on the reef resulted in structural injuries to the reef foundation.

In the last decade, multiple groundings on elkhorn and staghorn coral reefs have been reported in the USVI and Puerto Rico. Additionally, numerous orphan injury sites (unreported damage) have been discovered on coral reefs throughout both U.S. territories. In 2011 more than 35 vessel groundings or anchor impacts on or near coral reefs were reported throughout U.S. jurisdictions (20 in USVI and Puerto Rico combined, and more than 15 in Florida) (FDEP unpublished data, NOAA FKNMS unpublished data, NOAA Restoration unpublished data); however, it is likely two to three times that number go unreported.

Anchoring

Anchor (and chain) damage occurs in many areas. The size of the anchor, weather, and frequency of anchoring are directly related to the magnitude of the damage. In many areas with high tourist visitation, chronic anchor damage to coral reefs has been addressed by installing special mooring buoys that eliminate the need to anchor (Halas 1985, 1997). Fishing fleets that anchor in the same area for relief from adverse weather can also cause major localized damage, particularly to fragile staghorn corals (Davis 1977). In areas close to coral reefs that are designated for anchorage or frequently visited by large ships, damage can be significant. Anchors from large vessels may weigh several tons and are usually attached to the ship by a heavy chain. Heavy chains can drag across the reef as the ship responds to any change in the wind, tides, and currents, which results in dislodged and fractured corals

for hundreds of meters (Smith 1988). The 2008 revision of the U.S. Coast Guard rule designating the Port Everglades anchorage area in southeast Florida has resulted in fewer reports of anchor damage and vessel groundings associated with the anchorage.

Fishing

Fishing gear can be harmful to coral reefs. Derelict fishing gear can destroy benthic organisms and entangle both mobile and benthic fauna (e.g., Donohue et al. 2001), especially elkhorn and staghorn corals due to their branching morphology. Weighted gear deployed from the sea surface, such as traps, can damage corals if it lands directly on them or moves across the sea floor during retrieval or storm events (Lewis et al. 2009). This is particularly true in the case of storms that can mobilize traps and often snare buoy lines in branching corals such as elkhorn and staghorn corals. Lewis et al. (2009) reported that about 10 to 20 percent of the estimated 480,000 lobster traps annually deployed in the Florida Keys are lost, but the number increases to closer to 60 percent during years of high hurricane activity such as occurred in the 2005 to 2006 storm season. Trap movement during storms can bring these impacts even into protected, no-take zones. Miller et al. (2008b) noted that greater than 90 percent of the 78 patch reefs, including no-take zones, surveyed in the Florida Keys during June to August 2007 had remnants of lobster traps, and there were several instances of entanglement of staghorn coral colonies, resulting in tissue damage and breakage. Though fishers target areas of sand, rubble, or seagrass when deploying traps, each trap deployed in reef habitat can impact a mean of 198 cm^2 of surface area of fauna (Lewis et al. 2009). Although this area is relatively small, when multiplied by thousands of traps annually deployed and lost over the last 50 years, the cumulative impact is much greater.

Summary

The final listing rules (NMFS 2006, 2014) identified abrasion and breakage as a threat contributing to the threatened status of elkhorn and staghorn corals. Anthropogenic abrasion and breakage impacts to reefs are chronic and cumulative, occurring on an ongoing basis. Small, localized colony breakage likely occurs on a regular basis due to diver interactions, small vessel anchoring and groundings, and fishing. Impacts from large vessel groundings, towlines, and anchor impacts, while occurring with less frequency, often result in relatively large areas of injury. Ecologically, the region-wide threat of "Anthropogenic Abrasion and Breakage" to elkhorn and staghorn corals is thought to be low (2) due to the generally localized nature of this threat. However, the threat within U.S jurisdictions ranges from low (2) to medium (3). In Puerto Rico and USVI frequent shallow water vessel groundings pose a medium (3) threat for both elkhorn and staghorn corals, and frequent anchor impacts to staghorn coral in southeast Florida warrant a medium (3) ranking. Overall, while sometimes causing severe localized impacts from large vessels, anthropogenic physical impacts are not likely responsible for range-wide species declines, but left unabated, this threat is likely to impede recovery of these species (see Table 1).

Anthropogenic Abrasion and Breakage of Habitat	**Threat Ranking:**	**2**
	Impedes Recovery:	**Y**
	Listing Factor:	**A**

The final listing rule (NMFS 2006) identified anthropogenic abrasion and breakage as a threat contributing to the threatened status of elkhorn and staghorn corals through the present or threatened destruction, modification, or curtailment of its habitat or range (Factor A). Vessel groundings not only break individual coral colonies (see Anthropogenic Abrasion and Breakage of Species), but often result in large-scale habitat destruction. After larger vessel groundings, the impact site and surrounding reef are

often reduced to rubble. The loose rubble can cause continual abrasion and breakage to the surrounding reef, which is generally not conducive for natural recovery without active onsite restoration. Therefore, this threat (in relation to hard substrate habitat) can impede recovery of these species if left unabated. Given the relatively localized nature of this threat and potential for managing this threat, the ranking for this threat is low (2) in all areas for both species, except in Puerto Rico and USVI where several recent large vessel groundings, which have reduced reef structure to rubble, warrant a medium (3) ranking (see Table 1).

Nutrients (N, P)

Threat Ranking:	**SBU**
Impedes Recovery:	**Y**
Listing Factor:	**A,E**

The term nutrients, for purposes of this plan, refers to both organic and inorganic forms of the elements nitrogen (N) and phosphorus (P). This includes nitrate, nitrite, ammonium, and soluble reactive phosphate (inorganic forms) that are utilized by plants. It also includes dissolved organic nitrogen and phosphorus (including dissolved organic matter — DOM) that can be remineralized to inorganic forms that are available for plant assimilation.

Nutrients are largely recognized as elements that are beneficial for most organisms. Coral reefs, however, are adapted to low nutrient levels, and overabundance of nutrients can result in an imbalance that affects the entire ecosystem. Development of coastlines can result in the destruction of mangrove forests, which compounds the problem of anthropogenic nutrient runoff, as mangroves are able to filter massive amounts of nutrients and sediment caused by overdevelopment. Nutrient-rich water can enhance benthic algae and phytoplankton growth rates in coastal areas, and this may result in overgrowth, outcompetition, and algal blooms. Excess nutrient loads have been shown to affect coral physiology and the balance between corals and their endosymbiotic algae (zooxanthellae) (Szmant 2002). Increased levels of nutrients have also been shown to reduce growth rates in staghorn corals (Renegar and Riegl 2005) and compromise their health (Hodel and Vargas-Ángel 2007).

Organic nutrients in the form of DOM play a critical role in microbial biogeochemical processes (Hedges 2002). In the majority of marine ecosystems, the structure of the microbial community is highly dependent upon the chemical makeup of the DOM pool (Foreman and Covert 1999) such that corals are likely indirectly affected by DOM via their microbial interactions. Additional evidence strongly suggests that elevated or particular suites of dissolved organic compounds can alter the microbial community associated with corals, particularly within coral mucus (i.e., Surface Mucopolysaccharide Layer or SML) (Kuntz et al. 2005, Kline et al. 2006). The SML serves as a habitat for a suite of bacteria, including both beneficial and potentially pathogenic strains (Ritchie 2006). Nutrient effects could include stimulation of deleterious bacteria, including *Vibrio* spp. and other pathogens. Experimental enrichment studies on coral species (other than elkhorn or staghorn corals) with disease indicated that disease severity was substantially enhanced by nutrient augmentation adjacent to active disease lesions (Bruno et al. 2003).

Sources of nutrients include anthropogenic outlets, such as sewage and stormwater discharges and urban and farm runoff (Szmant 2002), submarine groundwater discharge (Slomp and van Cappellen 2004), and coastal aquaculture activities. Naturally occurring sources include leaf litter (Szmant 2002), excretion of digested planktonic biomass by sponges, and tidal upwelling events (Leichter et al 2003).

The final listing rule (NMFS 2006) identified nutrients as a threat contributing to the threatened status of elkhorn and staghorn corals. Likewise, the final rule maintaining elkhorn and staghorn coral as threatened species (NMFS 2014) lists nutrient over-enrichment as a threat contributing to the status of the species. It is widely understood that excess nutrients on coral reefs can lead to algal overgrowth and

competition if levels of herbivory are inadequate to remove excess algal production (see discussion in Loss of Recruitment Habitat). However, nutrient effects on corals (severity, magnitude, and source) are complex and highly debated. Furthermore, the effects of nutrient loads on acroporid physiology are currently unknown, relative to other stressors of elkhorn and staghorn corals. For this reason, while nutrients are recognized as a threat likely to impede the recovery of these corals, the ranking of "significant but unknown" (SBU) was provided to listed corals for all regions.

Contaminants

Threat Ranking:	**SBU**
Impedes Recovery:	**Y**
Listing Factor:	**E**

This section focuses on toxic and bioactive contaminants, whereas nutrients are discussed under the Nutrients threat assessment (see above). Contaminants are delivered to coral reefs via either point or non-point sources. Traditionally, studies of contaminants in coral reefs focused on the detection of substances in the environment or in the tissues of an organism (reviewed in Peters 1997). The analytical ability to detect contaminant substances at low concentrations (i.e., exposure) provides little insight on the effect these substances might have on the corals themselves (i.e., biological response). Histopathology and emerging tools such as gene expression (Edge et al. 2005) and biomarker analyses (Downs et al. 2005a) are beginning to provide the ability to evaluate the sub-lethal stress response and pathological consequences in corals exposed to contaminants. Developing an understanding of the toxicological effects of the high risk pollutants (i.e., effective concentrations, mode of impairment, and extent) on corals and coral reefs is needed.

Although frequently cited as affecting coral reef health, the concentration of chemical contaminants present in coral reefs is not well characterized, and even less is known regarding linkages between contaminants and coral condition. Low (parts per billion) concentrations of organic chemical contaminants including hydrocarbons (Negri and Heyward 2000), antifoulant Irgarol 1051 (Knutson et al. 2012), and pesticides (Negri and Heyward 2001), along with metals such as copper and zinc (Reichelt-Brushett and Harrison 2000, 2005) or iron (Vijayavel et al. 2012) can impact coral fertilization success and larval settlement. Downs et al. (2005) concluded that coral decline in a section of the northern Florida Keys is likely related to chemical contaminant exposure and noted that an analysis of contaminants present would greatly increase the power of determining the impact of this stressor. Rees et al. (1999) concluded that declines observed in coral community structure in Indonesia were the result of nearshore stresses, most likely from oils and other hydrocarbons. In southwest Puerto Rico, Pait et al. (2007) found a significant negative correlation between hydrocarbon (i.e., polycyclic aromatic hydrocarbons) concentrations and coral species richness (reef building species) on the reefs. A survey of environmental pollutants by Downs et al. (2011) in St. John, USVI showed that each of 6 study sites had different chemical profiles. In addition, corals had distinct cellular-stress marker patterns indicating different physiological impacts at each site. These findings emphasize the importance of local factors in contributing to coral and coral community declines.

Early studies of coral response to contaminant exposure focused on drilling muds, byproducts produced during offshore oil and gas exploration activities that can contain contaminants. Kendall et al. (1983) exposed staghorn coral to used drilling muds at varying concentrations, and determined that the coral response included reduced calcification and reduced tissue soluble protein levels after 24 hours exposure. These responses were more severe than in control treatments subjected to similar concentrations of inert particles (i.e., kaolin) and thus toxicity, not just turbidity, was imputed as causing this response.

More recently, Morgan and Snell (2002) examined responses (i.e., gene expression) of staghorn coral to the mosquitocide dibrom, which is widely used in the Florida Keys. Examining changes in gene expression of corals that are exposed to pesticides is a powerful way of determining whether the coral displays sub-lethal response to a given stressor in the absence of visible signs (e.g., bleaching or tissue loss). Morgan and Snell (2002) were able to develop molecular probes for two gene products that were induced by the pesticide exposure. One of these gene products appeared to be a generalized stress response, as it was induced by exposure to naphthalene and temperature extremes as well. However, the other transcript appeared to be specifically induced by organophosphate pesticides such as dibrom. Both of these stress-induced gene products were detected in naturally occurring staghorn colonies in the upper Florida Keys, suggesting that these organisms are detecting and responding to pesticides in their environment. The implication of this seemingly chronic stress response for coral survival, growth, reproduction, and recruitment is unknown.

Other recent dosing studies have detected impacts of pesticides or metals on photosynthesis (Jones and Kerswell 2003), fertilization, and settlement (Negri and Heyward 2001, Reichelt-Brushett and Harrison 2000) of different Pacific *Acropora* spp. Exogenous estrogen compounds at concentrations that occur in urban or sewage-affected coastal waters (i.e., 2 ng/L) have been shown to affect coral growth and fecundity (Tarrant et al. 2004), and *in situ* and laboratory experiments revealed that hard corals, including *A. cervicornis*, treated with various compounds found in common sunscreens experienced rapid and complete bleaching, even at extremely low concentrations (Danovaro et al. 2008). *Acropora cervicornis* has been shown to display higher susceptibility to copper toxicity than two other coral species tested with depressed photosynthesis, decreased growth, tissue accumulation, and other physiological changes observed at exposures as low as 4 ug/L (Bielmyer et al. 2010). While it is not surprising that toxic and biologically active substances impair corals, their effects are largely "silent," causing chronic and often sub-lethal stress or contributing to mortality of unapparent cause. It is also logical to assume that contaminants may have harmful effects in combination that would not be evident under exposure to an individual substance.

The final listing rule (NMFS 2006) identified contaminants as a threat contributing to the threatened status of elkhorn and staghorn corals though its magnitude of effect on the status is unknown. Given our level of knowledge about the effects of contaminants on elkhorn and staghorn corals, this threat is ranked as "significant but unknown" (SBU) as it is impossible to prioritize the level of threat posed by contaminants; however, there is compelling evidence in other organisms, including other coral species, that these compounds are present and do have devastating biological effects (Negri and Hayward 2000, 2001, Reichelt-Brushett and Harrison 2000), thereby making it possible that this threat is likely to impede recovery of these corals. This threat ranking is the same range-wide for both species (see Table 1).

Natural Abrasion and Breakage of Habitat	**Threat Ranking:**	**2**
	Impedes Recovery:	**N**
	Listing Factor:	**A**

As discussed earlier in this recovery plan (See Natural Abrasion and Breakage of Species), hurricanes and other storm events directly impact elkhorn and staghorn corals by breaking or removing coral colonies, as well as by mobilizing sediments and debris which abrade tissues and enhance exposure to any potential associated pathogens or contaminants. Storms can also affect habitat by covering available hard substrate with sediments and debris. The final listing rule (NMFS 2006) identified natural abrasion and breakage of habitat as a contributor to the status of the species through the present or threatened destruction, modification, or curtailment of its habitat or range (Factor A). Recent simulation work

predicts that in the presence of high grazing and absence of bleaching, coral populations are able to maintain themselves at all modeled levels of hurricane impact (Edwards et al. 2011). Therefore, the ART determined that it is unlikely that storms and hurricanes result in destruction or modification of coral habitat at a level that significantly contributes to the species' threatened status. Because hurricanes occur frequently and over a large geographic area, there is potential for natural abrasion and breakage of habitat to occur, but this threat is rated low (2) across all jurisdictions and throughout the ranges of these species due to its likely low impact on the species related to the other listed threats (see Table 1). Thus, it is unlikely that the threat of natural abrasion and breakage (in relation to hard substrate habitat) will impede recovery of these species if left unabated.

Offshore Oil and Gas Exploration

Threat Ranking: 1
Impedes Recovery: N

Offshore gas and oil exploration involves geophysical surveys, drilling to locate oil or natural gas reservoirs, and drilling of additional wells after a discovery to delineate a reservoir. It is a process to determine whether to proceed with development and production at a particular offshore site. "Offshore" refers to all waters and submerged lands seaward of the shoreline. Under the Outer Continental Shelf Lands Act (OCSLA), the Federal government has jurisdiction over the exploration and development of offshore resources, out to 200 nautical miles (NM) (307 km) from the shoreline (i.e., the Exclusive Economic Zone or EEZ). States have jurisdiction over any natural resources within 3 NM (5.6 km) of the shoreline, excepting Texas and the west coast of Florida where the Submerged Lands Act extends these States' jurisdiction in the Gulf of Mexico to 9 NM (16.7 km) (EIA 2005). Puerto Rico also has jurisdiction out to 9 NM (Minerals Management Service 2006). Because of the water depths in which elkhorn and staghorn coral grow, there are likely few locations where elkhorn and staghorn corals may possibly occur farther than 12 NM (22.2 km) from land (*Acropora* BRT 2005).

Potential threats to threatened corals and their habitat from oil drilling activities stem from spills and dumping of heavy metals (e.g., lead, chromium, mercury), drilling muds, and toxic chemicals. The specific effects on elkhorn and staghorn corals or on their habitat from such activities are not well known or well studied, but experiments indicate that both oil and chemical dispersants are toxic to coral larvae (Goodbody-Gringley et al., unpublished data, Ritchie, pers. comm.). Potential spills from drilling activities in the Gulf of Mexico and oil exploration off the northern coast of Cuba could impact listed corals in Florida if a spill becomes entrained in the Florida Current. The threat of oil and gas exploration was not identified as contributing to these species' extinction risk in the final rule listing elkhorn and staghorn coral as threatened (NMFS 2006) or in the final rule maintaining the two species as threatened (NMFS 2014). The threat posed to listed corals from oil and gas exploration activities is ranked as low (1) for the region (see Table 1). The threat is slightly higher (1.5) for Florida due to the proximity of current and anticipated drilling activity. Because oil-related activities are limited to refineries in Puerto Rico and USVI and there are no known oil exploration activities planned upstream, the threat ranking (1) is lower for these regions. Based on current levels of understanding and management regimes, offshore oil and gas exploration does not contribute to the status of the species and will not likely impede recovery of elkhorn and staghorn coral.

Sea Level Rise

Threat Ranking:	1
Impedes Recovery:	N
Listing Factor:	A

Sea level rise is a climate change impact that is likely to be less of a threat to elkhorn and staghorn corals than increases in temperature (See Temperature). Elkhorn coral generally inhabits a relatively narrow zone near the surface of the ocean. The species' rapid growth rate (when healthy) has allowed it to keep up with sea level rise during past periods of rapid climate change associated with deglaciation and warming (Fairbanks 1989, Pandolfi and Jackson 2006, Blanchon et al. 2009). Even at the most rapid trajectories of sea level rise, it is likely that elkhorn coral will be capable of keeping up, if conditions are otherwise suitable for its growth. Recent work in the Yucatan region of Mexico by Blanchon et al. (2009) indicates that during the warming that led to the last interglacial period, elkhorn coral was able to keep up with the first 3 m (9.8 ft) of rapid sea level rise. Continued sea level rise led to the demise of the original forereef crests. As sea level increased a total of 6 m (20 ft), elkhorn coral began to grow again at a more inland site. Whether or not elkhorn coral will be able to keep up with the first 3 m (9.8 ft) of future sea level rise will depend on abundance levels and its potentially reduced rate of growth due to local environmental stressors, bleaching, disease, and ocean acidification. Additionally, lack of suitable new habitat, limited success in sexual recruitment, coastal runoff, and coastal hardening (e.g., seawalls) will all work together to potentially limit the ability of elkhorn coral to keep up with rapid sea level rise.

In contrast, staghorn coral successfully inhabits a wider depth range and is less likely to suffer negative impacts from rising sea level. However, Blanchon et al. (2009) showed during the last interglacial period a transition of corals to a sediment-tolerant assemblage in the lagoon between the shoreline and reef crest. The new coral community included species most able to withstand sediment backwash during shoreline retreat — conditions not conducive to staghorn coral growth. Thus, while increases in depth due to sea level rise may not affect staghorn coral as much as elkhorn coral due to its more extensive depth range, similar to elkhorn coral, its ability to withstand sea level rise may be affected by other stressors associated with sea level rise such as increased sedimentation and coastal run-off. In summary, sea level rise may provide elkhorn and staghorn corals with access to some new habitats by raising water levels above existing reef flats and by shoreward expansion of coastlines. However, hardening of shorelines is likely to delay the progression of coastlines, and coastal inundation will release new sediments and pollutants into coastal waters (also seen in fossil evidence in Blanchon et al. 2009) potentially making these new habitats inhospitable to elkhorn and staghorn corals.

Sea level rise was identified in the final listing rule (NMFS 2006) as a threat contributing to the threatened status of the species through the present or threatened destruction, modification, or curtailment of their habitat or range (Factor A). The ART determined that overall, the influence of rising sea level on elkhorn and staghorn corals is likely to be relatively low given these species high growth rates, which allow them to keep pace with sea level rise; however, reductions in growth rate due to local stressors, bleaching, infectious disease, and ocean acidification may prevent these species from keeping pace. The final rule maintaining elkhorn and staghorn corals as threatened (NMFS 2014) did not find that sea level rise was a threat contributing to the status of the species. Because this threat is likely to have a relatively low effect on these species and their habitat, it is not likely to impede recovery of these species. Therefore, this threat is ranked as low (1) for all regions throughout these species' ranges (see Table 1).

Overharvest

Threat Ranking: 1
Impedes Recovery: N

As corals are not a food source, harvest of corals is mainly due to the continued demand for corals for use in aquaria or for decorative purposes. In general, the stony coral trade is dominated by exports from southeast Asia and the south Pacific (Bruckner 2000), and the U.S. imports 80 percent of the global trade in corals.

Elkhorn and staghorn corals are protected by a variety of state, federal, and international regulations prohibiting their collection, sale, transport, or trade. Elkhorn and staghorn coral are protected under CITES as Appendix II species. Appendix II species may be authorized for export when specimens were legally acquired and export will not be detrimental to the species' survival.[3] All foreign nations (except Haiti) within the range of elkhorn and staghorn corals are parties to CITES; however, not all of these parties have national laws or regulations prohibiting collection of corals. For a summary of trade and collection laws for the U.S. and for individual Caribbean nations, see Appendix A.

Within the United States, commercial coral collection has been banned in State of Florida waters since 1974 (Jaap 1984; Florida Admin. Code Ann. 68B-42.009(1)), and this ban was extended to U.S. territorial waters in the Gulf of Mexico and U.S. South Atlantic (50 CFR § 622.4(a)(1),(3)). The collection of all corals (dead or alive) also is prohibited in Puerto Rico (P.R. Law No. 147) and USVI (12 VIC §106(c)(1)). Historically, shell and curio shops sold colonies of elkhorn and staghorn but usually claimed that specimens were collected in Haiti (Porter 1987). The ESA 4(d) regulations specifically prohibit take, import, export, and all commercial activity for elkhorn and staghorn corals (73 FR 64264). However, collection likely occurs on a relatively small scale, even with existing regulations in place.

Given that existing regulations in the U.S. prohibit collection and trade of elkhorn and staghorn corals and that coral trade is dominated by exports from southeast Asia and the south Pacific, the threat of overharvest to the recovery of these corals is ranked as low (1) throughout their ranges (see Table 1). Neither final listing rule (NMFS 2006, 2014) identified overharvest as a factor contributing to the species' threatened status.

Overgrowth Competition

Threat Ranking: 1
Impedes Recovery: N
Listing Factor: E

In the final listing rule (NMFS 2006), competition was identified as a threat contributing to the status of the species under Factors A and E. Competition was classified as a minor contributor to the status of the species under Factor E due to the extremely reduced population size of the two species. Competition was also identified as a factor contributing to the species' threatened status through the present or threatened destruction, modification, or curtailment of their habitat or range (Factor A). However, the recovery plan calls this threat "Loss of Recruitment Habitat" rather than competition. Overgrowth competition as described in this section is intended to capture only the direct overgrowth impacts of other benthic organisms on existing elkhorn and staghorn coral colonies (Factor E).

Coral reefs are described as space-limited systems, and it is believed that competition for space is an important structuring factor for reef communities; however, elkhorn and staghorn corals have relatively high growth rates (for corals) and a tree-like morphology that makes them less susceptible to overgrowth by other encrusting or mat-forming organisms. Additionally, although overgrowth

[3] A CITES permit is not required for dead coral specimens less than 30 mm (1.3 in) in size.

competition can occur (e.g., by macroalgae such as *Halimeda* or *Lobophora*, or encrusting invertebrates such as *Erythropodium* spp.), it usually affects only small areas of the basal tissue margins on the colony.

The final listing rule (NMFS 2006) named competition as a minor contributor to the threatened status of the species due to the extremely reduced population size of the two species. The ART determined that because overgrowth competition has a minor effect on the two species, it is not contributing to their threatened status. If left unabated, it is not likely to impede recovery. The final rule maintaining elkhorn and staghorn species as threatened (NMFS 2014) did not find competition to be a factor affecting the status of the species. Therefore, this threat is ranked low (1), with a slightly higher rank (2) assigned to staghorn coral populations in southeast Florida due to persistent cyanobacterial blooms in this region. The more important competitive effects of macroalgae and other benthic organisms in pre-empting space for recruitment of new colonies are captured under the Loss of Recruitment Habitat stressor (see above).

Sponge Boring

Threat Ranking:	**1**
Impedes Recovery:	**N**
Listing Factor:	**E**

A group of excavating sponges of the family Clionaidae (three species, vis. *C. aprica* Pang, *C. caribbaea* Carter and *C. tenuis* (Zea and Weil 2003)) play a critical role in space monopolization of coral reef substrata where they compete aggressively with corals and other organisms for illuminated space (Lope-Victoria and Zea 2004). Different species of *Cliona* have differing levels of impact ranging from devouring entire live standing colonies to invading elkhorn and staghorn coral skeletons from dead margins. Thus, these sponges can impose direct tissue and colony mortality as well as increase the rate of branch fragmentation, consequently dispersing the sponge itself (Lope-Victoria and Zea 2004). Although these species excavate and penetrate only the first 1.5-2 cm (0.6-0.8 in) of the substratum, they are capable of spreading laterally at rates of 9-18 cm/yr (3.5-7 in/yr) (Acker and Risk 1985, Rutzler 2002, Zea and Weil 2003).

In Puerto Rico and, to a lesser extent, Navassa, clionid sponges monopolize much of the exposed substrata that were formerly occupied by live elkhorn coral and actively overgrow and kill standing elkhorn coral colonies and fragments. For example, Weil et al. (2002) noted that on average 16 percent of the colonies from three reefs in La Parguera were being overgrown by clionid sponges, advancing at an average rate of 9 cm/year (3.5 in/yr). Off Mona Island, a total of 22 percent of all restored fragments at the *Fortuna Reefer* grounding site (approximately 6.8 acres of impact) were killed by *Cliona* spp. over a ten year period (Bruckner et al. 2008). As of February 2008, over 30 percent of shallow forereef substrates (0-3 m depth; 0-9.8 ft), including dead standing colonies, were colonized by *Cliona,* and over 5 percent of remaining live corals were losing tissue to this sponge (Bruckner et al. 2008).

The final listing rule (NMFS 2006) identified the threat of sponge boring as a minor contributor to the threatened status of the species due to their reduced population size. *Cliona* appears to be a low-medium threat (2) to elkhorn coral in Puerto Rico and of minimal importance (1) throughout the range for both species. Thus, the ART determined that sponge boring is not significantly contributing to the status of the species and would not impede recovery if left unabated (see Table 1). The final rule maintaining elkhorn and staghorn corals as threatened (NMFS 2014) did not find that sponge boring was a threat contributing to the status of the species.

African Dust

Threat Ranking:	0.5
Impedes Recovery:	N
Listing Factor:	E

Shinn et al. (2000) proposed that atmospheric dust transported largely from Africa has severely affected Caribbean coral-reef organisms by acting as a vector for pathogens such as *Aspergillus sydowii*, a fungus known to be a pathogen affecting two sea fans *(Gorgonia ventalina* and *G. flabellum)* (Geiser et al. 1998). Recent research, however, found that of seven species of *Aspergillus* present in dust samples collected from Mali and St. Croix, USVI, *A. sydowii* was not present (Rypien 2008). Several other studies that examined the fungal biota of African dust also did not detect *A. sydowii*, although several other species of *Aspergillus* were present (Griffin et al. 2003, Shinn et al. 2003, Kellogg et al. 2004, Weir-Bush et al. 2004). These data taken in conjunction with recent molecular evidence suggest that African dust as a source of the marine pathogen *A. sydowii* should be considered unlikely (Rypien 2008). To date, the identified *(Serratia marcescens)* or suspected *(Vibrio charcharia)* pathogens of elkhorn and staghorn corals have not been identified among the microbes in dust (Griffin et al. 2002).

The final listing rule (NMFS 2006) identified the threat of African dust as a minor contributor to the status of the species due to their reduced population size. The ART determined that African dust is not likely contributing to the status of the species since suspected pathogens of elkhorn and staghorn corals have not been found in African dust. However, because the lack of identification of causative pathogens for many coral diseases impedes the ability to determine if disease pathogens are carried in African dust, this threat was ranked as low (0.5) for all areas throughout the ranges of elkhorn and staghorn corals. If left unabated, this threat is not likely to impede recovery of these species (see Table 1). The final rule maintaining elkhorn and staghorn corals as threatened (NMFS 2014) did not find that African dust was a threat contributing to the status of the species.

Alien Species

Threat Ranking:	P
Impedes Recovery:	N

Alien species are defined as any invasive, non-indigenous species (plant, animal, or microbe) that may adversely affect ecosystems they invade. Adverse impacts may result from virulence (in the case of microbes), production of harmful compounds, or rapid growth and/or reproduction allowing invaders to out-compete native species for resources. Research suggests that increasing temperatures may trigger even greater expansion in the range and types of invasive species (Rocha et al. 2005). There are numerous examples of invasive species in the Gulf of Mexico and South Atlantic regions (http://www.gsarp.org), but little to nothing is known of invasive microbial species.

Invasive lionfish, *Pterois miles* and *P. volitans,* may have the potential to negatively affect staghorn and elkhorn recovery. Lionfish are native to the Indo-Pacific but have spread rapidly into the western north Atlantic and Caribbean over the last two decades. Because they are not native, they have no natural predators in the Caribbean, but there have been reports of predation of lionfish by groupers (Maljković et al. 2008, Mumby et al. 2011). Lionfish are generalist piscivores that have been observed to feed on over 40 species of teleost fish, including herbivores such as parrotfish (Morris and Akins 2009, Côté and Maljković 2010, Green et al. 2011). Lionfish have been implicated as a contributor to the shift to macro-algal dominance on mesophotic (30-150 m depth) reefs in the Bahamas through predation of herbivores (Lesser and Slattery 2011). Thus, it is possible that the presence of lionfish may impact the availability of *Acropora* recruitment habitat by predation of important reef grazers that aid in keeping algal cover under control. However, the effects of lionfish on coral reef habitat remain largely unstudied. The final rules listing and maintaining elkhorn and staghorn corals as threatened (NMFS 2006, 2014) did not

evaluate the effects of alien species on their status. Because the number, sources, and impacts on elkhorn and staghorn corals are currently unknown at both local and regional scales, alien species are currently listed as potential threats (P), which at current levels of knowledge are not likely to contribute to the status of the species or impede recovery of listed corals (see Table 1).

H. Conservation Measures

Currently, hundreds of conservation efforts intended to reduce or remove threats to coral reefs, in general, are being conducted by individuals, private organizations, state/territorial and local agencies, and federal agencies. Such efforts include (but are not limited to) legislative and policy advocacy for coral reef conservation; mapping, monitoring, and assessment of coral reefs; mooring buoy and coral reef demarcation programs; research on coral disease, toxicology, microbiology, genetics, and reproduction; outreach and education about human impacts on coral reefs through printed media, public events (local, regional, and international), and volunteer programs; and physical restoration of degraded coral reefs (e.g., transplanting corals to avoid impacts from coastal development projects, reattaching coral fragments after storms and/or vessel groundings). All of these efforts contribute to the conservation of elkhorn and staghorn corals as these species are often found on or near the coral reefs targeted by these projects. Additionally, with the listing of these corals as threatened, individual coral reef conservation efforts increasingly focus on these two species. Unfortunately, inconsistent and limited funding, restricted geographic scales, weak government support, limited public participation and awareness, and patchwork cooperation and coordination continue to hinder the success of these efforts at the range-wide scale of elkhorn and staghorn coral populations. Because the threats that these corals face are not only local (e.g., point source pollution, individual coastal development projects, vessel groundings), but regional (e.g., non-point source pollution, aggregated effect of multiple coastal development projects) and global (e.g., climate change) in scale, individual conservation efforts at the local scale are not adequate for abatement of these threats.

Despite the limited overall success of existing efforts in conserving elkhorn and staghorn corals on a range-wide scale, local and regional efforts have resulted in the development of best management practices (e.g., Best Management Practices (BMPs) for Construction, Dredge and Fill and Other Activities Adjacent to Coral Reefs (PBS&J 2008)), improved response and restoration techniques for physical injuries, coordinated outreach campaigns, improved habitat maps, and a large amount of research data. Thus, current conservation efforts offer a significant foundation for successfully implementing recovery actions via the knowledge, experience, and readiness of existing organizations and agencies already working on behalf of Atlantic/Caribbean coral reefs and these listed coral species.

II. RECOVERY STRATEGY

The purpose of this recovery plan is to identify a strategy for rebuilding and assuring the long-term viability of elkhorn coral and staghorn corals in the wild, allowing ultimately for their removal from the federal list of endangered and threatened species. Elkhorn and staghorn coral populations should be large enough so that successfully reproducing individuals, including thickets, comprise numerous populations across the historical ranges of these species and should be large enough to protect their genetic diversity and maintain their ecosystem function. Threats to these species and their habitat must be sufficiently abated to ensure a high probability of survival into the future.

A. Key Facts and Assumptions

Historically, elkhorn and staghorn corals were dominant species in Atlantic/Caribbean coral reefs that were able to thrive in variable environmental conditions during the Holocene including high temperatures, variable salinity, hurricanes, and rapid sea level rise (Greer et al. 2009). Disease, temperature-induced bleaching, and hurricanes have caused a drastic decline in abundance of these species within the past 30 years. Based on spatially and temporally limited quantitative data, an estimated 97 percent decline in these species' abundance has occurred. It is unclear whether local extirpations (e.g., at an island-wide or national scale) have already occurred undetected.

In addition to a lack of baseline abundance and distribution data, there is a lack of adequate demography and genetics information for both species, particularly for the previously robust populations and to a lesser extent for current remnant populations. Demographic and genetic uncertainties result in inadequate models to predict responses of extant populations to future disturbances and threats with any confidence. Virtually no quantitative information on sexual or asexual recruitment rates of robust, pre-1980s populations is available. However, given the dominance of these two species before their decline, recruitment rates were presumably high enough to be able to maintain abundant populations. The decline in density of current populations and low genotypic diversity in some locations has likely reduced fertilization success and larval supply because self-fertilization does not occur in these two species. Reduced colony density has probably led to reduced asexual recruitment, both through the reduction in available material able to break off and establish new colonies and the reduction in thickets which aid in fragment retention in the complex structure. Thus, reduced abundance has likely compromised both sexual and asexual recruitment success. Genetic studies suggest that no population is more or less significant (in terms of recruitment sources) to the status of these species and that there is limited capacity for re-seeding of populations across long distances (greater than 500 km) (Baums et al. 2005a, 2006, 2010, Vollmer and Palumbi 2007). Population studies also indicate that coral populations in certain geographic regions, such as elkhorn in the Florida Keys, are particularly vulnerable based on minimal genotypic diversity (thus limiting potential for acclimation/adaptation to environmental disturbances) and low levels of sexual recruitment (Baums et al. 2006, Williams et al. 2008).

Some of the dominant threats to elkhorn and staghorn coral recovery are relatively "unmanageable" events, including disease, rising ocean temperature, and hurricanes, as they are, in part, naturally occurring phenomena. Reasonable expectations are that increases in temperature and storm intensity will continue unabated or worsen in the coming decades in response to current and expected future emissions of greenhouse gases into the atmosphere. There is more uncertainty regarding the root causes of coral disease. Specific etiological agents have been elusive, and many factors and co-factors may contribute to disease manifestation rather than one distinct agent (Wobeser 1994, Lesser et al.

2007). The contribution of chronic and/or sub-lethal conditions to overall coral health is also relatively unknown and visually undetectable. At the population level, chronic and sub-lethal disease effects may manifest as reduced reproductive output, reduced larval recruitment or survival, and retarded growth in elkhorn and staghorn corals.

There is growing evidence that synergistic effects of disease, temperature-induced bleaching, and hurricanes, in combination with each other or with more moderately ranked threats, such as anthropogenic physical damage, nutrients, contaminants, sedimentation, competition, and predation, exacerbate impacts and affect the persistence of elkhorn and staghorn coral. There are observations from diverse geographical locations of coral disease outbreaks following hurricane disturbances (Puerto Rico, Bruckner and Bruckner 1997; Navassa, Florida Keys, Miller and Williams 2006, Williams et al. 2008; Bonaire, Bruckner pers. comm. 2002; Curacao, Vermeij pers. comm. 2002; Honduras, Halley et al. 2001); however, there is no evidence regarding the mechanism(s) that may explain this linkage of hurricanes and disease impacts. Predators of elkhorn and staghorn corals can also serve as vectors for disease (Williams and Miller 2006). Additionally, several authors demonstrated a link between increased coral disease prevalence and/or virulence and increased temperature (Harvell et al. 1999, Patterson et al. 2002), and Muller et al. (2008) demonstrated a strong linkage between temperature-induced bleaching and subsequent disease-induced mortality in elkhorn coral following the 2005 bleaching event in the USVI. Ritchie (2006) showed reduction in naturally occuring antibiotic activity on healthy coral under bleaching conditions. Further, Mao-Jones et al. (2010) provided evidence that a shift to a pathogen-dominated microbial community, from transient stressful conditions, can persist long after environmental conditions have abated, leading to a long-term loss of innate defenses. Land-based runoff, pollution, or other local stressors may exacerbate bleaching impacts by lowering the thermal threshold when corals bleach (i.e., increasing their susceptibility) and/or increasing the duration of impaired growth after a bleaching event (Wooldridge 2009, Carilli et al. 2009). Similarly, Bruno et al. (2003) found that nutrient enrichment caused increased disease-associated tissue loss in corals. There are anthropogenic sources (i.e., sewage) of some coral disease-causing bacteria (Patterson et al. 2011).

The ART reached the following conclusions:

1) Low population sizes and Allee effects necessitate strategic population enhancement actions for recovery. Current low population sizes of elkhorn and staghorn corals throughout much of the wider Atlantic/Caribbean have several implications, already summarized by the *Acropora* BRT (2005).

> First, the number of sexual recruits to a population will be most influenced by larval availability, recruitment, and early juvenile mortality. Because corals cannot move and are dependent upon external fertilization in order to produce larvae, fertilization success declines greatly as adult density declines; this is termed an Allee effect (Levitan 1991). To compound the impact, *Acropora* spp., although hermaphroditic, do not effectively self-fertilize; gametes must be outcrossed with a different genotype to form viable offspring. Thus, in populations where fragmentation is prevalent, the effective density (of genetically distinct adults) will be even lower than colony density. It is highly likely that this type of recruitment limitation (Allee effect) is occurring in some local elkhorn and staghorn populations, given their state of drastically reduced abundance/density. Simultaneously, when adult abundances of elkhorn and staghorn corals are reduced, the source for fragments (to provide for asexual recruitment) is also compromised. These conditions imply that once a threshold level of population decline has been reached (i.e., a density where fertilization success becomes negligible) the chances for recovery are low.

2) Further worsening the chances of successful recruitment, habitat modification, associated with coastal development, sedimentation, and benthic algal overgrowth, is likely compromising the availability of appropriate habitat for successful sexual and asexual recruitment and is subjecting recruitment to further reductions. Without successful recruits, these species cannot sustain, let alone increase, their abundance, distribution, or genetic diversity.

3) Threats related to CO_2 emissions (warming and acidification) are overarching and require action at federal and international levels. Further mortality from bleaching and other warming-related impacts (e.g., disease, hurricanes) are expected to occur even if CO_2 emissions are curtailed, due to the time lag between CO_2 emissions into the atmosphere and attaining atmosphere/ocean equilibrium. Thus, local mitigation strategies and *ex situ* conservation actions must be pursued.

4) Reducing more moderately ranked local threats (e.g., nutrients, contaminants, sedimentation) is essential for recovery of elkhorn and staghorn corals given the synergistic effects of myriad threats. Reduction of local threats will allow corals to expend more energy for acclimation/adaptation to offset the effects of worsening global stresses.

5) At current levels of impact, diseases affecting elkhorn and staghorn corals are expected to significantly reduce the probability of their survivial and recovery in the wild. Effective disease control or management strategies for elkhorn and staghorn corals are not currently available due to the lack of specific mechanistic and predictive understanding. However, as discussed above for warming, the reduction of more moderately-ranked threats can help by reducing overall stress that may aid in strengthening innate defenses and resistance to disease.

B. Primary Focus and Justification of Recovery Efforts

The proposed recovery approach addresses the most pressing gaps in knowledge, addresses critical demographic factors required for recovery, and targets the reduction or elimination of threats so that the recovery goal outlined in this plan has the greatest likelihood of being achieved. Because many of the important threats to the recovery of elkhorn and staghorn corals are not directly manageable, the recovery strategy must pursue simultaneous actions to:

a) Improve understanding of population abundance, trends, and structure through monitoring and experimental research.

b) Develop and implement appropriate strategies for population enhancement through restocking and active management, in the short to medium term, to increase the likelihood of successful sexual reproduction and to increase wild populations.

c) Implement ecosystem-level actions to improve habitat quality and restore keystone species and functional processes such as herbivory to sustain adult colonies and promote successful natural recruitment in the long term.

d) Curb ocean warming and acidification impacts to health, reproduction, and growth, and possibly curb disease threats, by reducing atmospheric greenhouse gas concentrations.

e) Reduce locally-manageable stress and mortality threats (e.g., predation, anthropogenic physical damage, acute sedimentation, nutrients, contaminants).

f) Determine coral health risk factors and their inter-relationships and implement mitigation or control strategies to minimize or prevent impacts to coral health.

III. RECOVERY GOAL, OBJECTIVES, AND CRITERIA

A. Goal

The goal of this recovery plan is to increase the abundance and protect the genetic diversity of elkhorn and staghorn coral populations throughout their geographical ranges while sufficiently abating threats to warrant delisting of both species.

B. Recovery Objectives and Criteria

The Recovery Goal can be subdivided into discrete component objectives that, collectively, describe the conditions necessary for achieving the Recovery Goal. The ART identified two Recovery Objectives: 1) Ensure population viability, and 2) Eliminate or sufficiently abate global, regional, and local threats that contribute to the species' status.

Section 4(f) of the ESA directs the development and implementation of recovery plans. These plans must contain, to the maximum extent practicable, objective, measurable Recovery Criteria which, when met, would result in a determination that these species be removed from the List of Endangered and Threatened Wildlife. Recovery Criteria may include such things as population numbers and sizes, specific habitat conditions, and management or elimination of threats by specific mechanisms. Recovery Criteria can be viewed as targets, or values, by which progress toward achievement of Recovery Objectives can be measured. Recovery criteria may be refined based on new information including species status and vulnerability to threats.

The ART framed the Recovery Criteria in terms of both population parameters (Population-based Recovery Criteria) and the five listing factors (Threat-based Recovery Criteria). The Population-based Recovery Criteria (Criteria 1-3) represent what recovered species would look like. The Threat-based Recovery Criteria (Criteria 4-10) represent the conditions needed to abate threats contributing the the species' extinction risk sufficiently to allow them to sustain recovered species. The Recovery Criteria are based on current literature, identified assumptions, and expert consensus. In some cases, the current best available information is so limited that it is not practicable to identify delisting or reclassification criteria. Thus, interim criteria are identified that require obtaining the information necessary to establish the criteria associated with certain recovery objectives. Once the information is acquired, interim criteria will be replaced with final criteria that reflect the conditions necessary to achieve the recovery objectives.

The Recovery Criteria in this plan are those the ART believe meet the ESA's requirement for objective, measurable criteria to address the species' status and the causal listing factors in section 4 of the Act, based on information available at present to judge the species' progress toward recovery. However, recovery under the ESA is an iterative process with periodic analyses required to provide feedback into species' listing status and progress toward recovery. The ESA requires a review of the status of each listed species at least once every five years after it is listed. Periodic review of the species may lead to updates or revisions of the recovery plan, changes in the listing status of the species, or delisting. While meeting all of the recovery criteria would indicate that the species should be delisted, it is possible that delisting could occur without meeting all of the recovery criteria if the best available information indicated that the species no longer met the definition of endangered or threatened. In the case of elkhorn and staghorn corals, it is possible that because of the interaction between the threats and the species' population responses, fully achieving all of the Threat-based Recovery Criteria may not be necessary to achieving restored, sustainable populations if the benefits to the species from successfully

addressing one threat (e.g., nutrient enrichment) make them more highly resilient to another threat (e.g., disease). Changes to the species' status and delisting would be made through additional rule-making after considering the same five ESA factors considered in listing decisions, taking new information into account.

The following criteria are not listed in order of priority. Some of the criteria are identical for both species; for others, different parameters are provided for each species.

Objective 1: Ensure Population Viability

The recovery strategy for elkhorn and staghorn corals requires simultaneous increases in recruitment and abundance of large colonies while maintaining genetic diversity. The following criteria are population-based and measure whether stable, abundant, and genetically diverse populations of elkhorn and staghorn corals are present throughout their geographic ranges.

Population-Based Recovery Objectives and Criteria

Criterion 1: Abundance

Elkhorn coral: Throughout approximately 10 percent of consolidated reef habitat in 1 to 5 m water depth within the forereef zone, achieve a density of 0.25 colonies ≥ 1 m diameter in size per m^2, or achieve approximately 60 percent live elkhorn coral cover. Populations with these characteristics should be present throughout the range and maintained for 20 years;

and

Staghorn coral: Throughout approximately 5 percent of consolidated reef habitat in 5 to 20 m water depth within the forereef zone, achieve a density of 1 colony ≥ 0.5 m diameter in size per m^2, or achieve approximately 25 percent live staghorn coral cover. Populations with these characteristics should be present throughout the range and maintained for 20 years.

This criterion is based on the understanding that elkhorn and staghorn coral thickets (i.e., high density stands) characterized populations prior to initial declines and are necessary to fulfill ecological functions of reef habitat provision and fragment retention. This criterion requires persistent, healthy (i.e., high tissue cover) thickets to occupy a small portion of potential core habitat strata with the assumption that, under this condition, additional, lower-density stands would occupy additional habitat area. The colony size, density, amount of habitat, and live coral cover values are different for each species due to their differences in morphology and habitat occupation. Criterion values were derived from data available for existing high density stands (Vargas-Angel et al. 2003, Baums et al. 2006, Miller unpublished data).

Criterion 2: Genotypic Diversity

Maintain current overall average genotypic diversity (proportion of unique genotypes per number of colonies sampled) of approximately 0.5 across these species' range.

This criterion requires that current levels of genotypic diversity be maintained on average throughout these species' ranges (based on measured, range-wide estimate for elkhorn coral, Baums et al. 2006). A genotypic diversity equal to one would be indicative of purely sexual recruitment as all sampled colonies would have a unique genotype. A genotypic diversity approaching zero would be indicative of predominantly asexual recruitment. Thus, a genotypic diversity of 0.5 indicates a balance between sexual and asexual recruitment. It is recognized that considerable variability in this parameter among sites is expected, but basic levels of genotypic diversity are required on the scale of species as a whole since high genotypic diversity may provide a greater ability to withstand environmental variability and disease.

Criterion 3: Recruitment

Observe recruitment rates necessary to achieve Criteria 1 and 2 over approximately 20 years;

and

Observe effective sexual recruitment (i.e., establishment of new larval-derived colonies and survival to sexual maturity) in each species' population across their geographic range.

Successful recruitment is essential for recovery of these two species and for re-establishing the high abundances once present throughout their ranges. Because of the propensity of these two species to fragment, asexual reproduction is likely to be the major avenue of recruitment. However, sexual recruitment is necessary for overcoming depensatory population effects and providing genetic variation important for adapting to changing environmental conditions. A lack of information on historical and current sexual recruitment rates of elkhorn and staghorn corals hinders the ability to define a quantitative criterion needed for recovery. Thus, the second part of the recruitment criterion acknowledges the need for observable sexual recruitment of larvally derived colonies that survive to sexual maturity and contribute to reproduction.

Objective 2: Eliminate or sufficiently abate global, regional, and local threats

The recovery strategy for elkhorn and staghorn corals requires simultaneous reduction in threats across their geographic range. While each threat-based criterion influences the species' viability, there are also complex interactions and inter-relationships of threats and population response, which will require evaluation as the recovery plan is implemented. The following criteria are based on the threats affecting the status of both listed coral species (see Table 1) and measure whether each of the threats that are currently or are expected to impede recovery of these species is sufficiently abated. While meeting all of the recovery criteria would indicate that the species should be delisted, it is possible that delisting could occur without meeting all of the recovery criteria if the best available information indicated that the species no longer met the definition of endangered or threatened. In the case of elkhorn and staghorn corals, it is possible that because of the interaction between the threats and the species' population responses, fully achieving all of the Threat-based Recovery Criteria may not be necessary to achieving restored, sustainable populations if the benefits to the species from successfully addressing one threat (e.g., nutrient enrichment) make them more highly resilient to another threat (e.g., disease). Changes to the species' status and delisting would be made through additional rule-making after considering the same five ESA factors considered in listing decisions, taking new information into account.

Threat-Based Recovery Objectives and Criteria

Interim Criterion 4: Disease (Listing Factor C)

Develop a quantitative recovery criterion through research. Based on 5 years of data, a criterion will be established to reduce the impact of disease to a level appropriate for recovery.

Because there is a lack of information concerning the abundance of both elkhorn and staghorn corals throughout their ranges and concerning the extent of the effects of disease on elkhorn and staghorn coral colonies, this interim criterion was developed. Once baseline levels of disease (e.g., seasonal prevalence and incidence, transmission, rate/amount of tissue loss, and mortality) have been determined in robust reference populations, a measurable criterion for determining whether the threat of disease has been abated can be developed.

Criterion 5: Local and Global Impacts of Rising Ocean Temperature and Acidification (Listing Factor E)

Sea surface temperatures across the geographic range have been reduced to Degree Heating Weeks less than 4;

and

Mean monthly sea surface temperatures remain below 30°C during spawning periods;

and

Open ocean aragonite saturation has been restored to a state of greater than 4.0, a level considered optimal for reef growth.

Frequent episodes of high ocean temperature directly threaten the survival and recovery of elkhorn and staghorn corals through the disruption of both the coral-symbiont relationship, resulting in coral bleaching and subsequent mortality, and coral reproductive success. Coral bleaching is caused by an accumulation of thermal stress over time. Mass coral bleaching commonly occurs when thermal stress levels reach 4 Degree Heating Weeks (Eakin et al. 2009). Six significant Caribbean bleaching events involving mass coral mortality have occurred since 1983, far too frequent for reefs to recover (Baker et al. 2008, Eakin et al. 2010). Thus, the frequency of these thermal-stress events needs to be reduced to allow time for coral recovery between events. Additionally, ocean temperatures above 30°C greatly decrease larval survivorship and settlement of elkhorn coral (Randall and Szmant 2009). Therefore, mean monthly sea surface temperatures likely need to be below 30°C during spawning periods to improve successful coral reproduction. Along with these temperature conditions, optimal growth of these corals occurs at or above an open ocean aragonite saturation state of approximately 4.0. At lower aragonite saturation states, calcification and coral growth rates decrease. The current open ocean aragonite saturation state in the Caribbean has decreased to less than 3.8; an open ocean aragonite saturation state below approximately 3.0 will result in most reefs shifting to a net erosional state (Hoegh-Guldberg et al. 2007).

Criterion 6: Loss of Recruitment Habitat (Listing Factor A)

Abundance (Criterion 1 above) addresses the threat of Loss of Recruitment Habitat because the criterion specifies the amount of habitat occupied by the two species. If Criterion 1 is met, then this threat is sufficiently abated;

or

Throughout the ranges of these two species, at least 40 percent of the consolidated reef substrate in 1-20 m depth within the forereef zone remains free of sediment and macroalgal cover as measured on a broad reef to regional spatial scale.

Acropora species' critical habitat has been identified as substrate of suitable quality and availability to support larval settlement and recruitment and reattachment and recruitment of asexual fragments. Substrate of suitable quality and availability was defined as natural consolidated hard substrate that is free from fleshy or turf macroalgal cover and sediment cover. The purpose of critical habitat is to ensure that amounts of suitable habitat needed for successful coral recruitment are protected from destruction or adverse modification resulting from federal activities (activities funded, authorized or implemented by federal agencies). This recovery criterion will ensure that sufficient recruitment habitat is available for recovery of the species. The value was chosen from simulation models reported in Mumby et al. (2007a) and Hoegh-Guldberg et al. (2007) that predict that at least 40 percent of the substrate on Caribbean reefs with approximately 10-20 percent coral cover needs to be grazed by herbivores for habitat conditions on these reefs to be conducive for coral recovery from disturbance events (see Fig. 14). It is recognized that habitat characteristics important to settlement of larvae and reattachment of asexual recruits is on the scale of millimeters to centimeters, but this criterion is designed to ensure the availability of habitat on a broader reef to region scale. Over the past several decades, there has been a phase shift from coral dominated to algal dominated reefs throughout the Caribbean, which has led to a reduction in availability of suitable recruitment habitat. This criterion is intended to be an indicator of the habitat characteristics necessary to promote the return to a coral dominated state, which will support acroporid settlement and recruitment.

Interim Criterion 7: Nutrients, Sediments, and Contaminants (Land-Based Sources of Pollution) (Listing Factor E)

Develop quantitative recovery criteria through research. Based on 5 years of data, criteria will be established to reduce sources of nutrients, sediments, and contaminants to levels appropriate for recovery.

Nutrients, sediments, and contaminants are known to negatively impact corals. However, there is a lack of information tying presence of these pollutants on reefs to coral condition and a lack of information regarding thresholds of tolerance to these threats. Once baseline information on levels of these pollutants in robust reference populations has been determined, a measurable criterion for determining whether the threat of land-based sources of pollution has been abated can be developed. See also Criterion 3: Recruitment. Observing increased, effective recruitment in elkhorn and staghorn corals will likely be an indication that the threats from nutrients, sediments and contaminants have been abated. See also Criterion 6: Loss of Recruitment Habitat. Observing sufficient availability of habitat suitable for recruitment is also a likely indication that this threat has been abated.

Criterion 8: Regulatory Mechanisms (Listing Factor D)

Adequate domestic and international regulations and agreements are adopted as applicable to ensure that all threat-based criteria are met.

For example, appropriate local, state/regional, national, international, and multi-jurisdictional efforts, agreements, and regulations are necessary to abate the threats from LBSP, physical impacts to corals, and rising sea surface temperatures and ocean acidification resulting from increasing atmospheric CO_2 concentrations.

As discussed in several of the other threat-based criteria, regulations (and enforcement of those regulations) are necessary to achieve the recovery objectives. In some cases, the regulatory framework exists, but policy specifically addressing threats to corals and coral reefs (e.g., water quality standards) is needed. Additionally, area-based management efforts that incorporate coastal, marine, and upland areas, which are interconnected though often separately managed, are necessary to address the multiple uses and threats facing elkhorn and staghorn corals.

Criterion 9: Natural and Anthropogenic Abrasion and Breakage (Listing Factor E)

Appropriate and effective regulatory, response, restoration, and enforcement mechanisms are in place domestically and internationally for both planned and unplanned impacts. For planned impacts (e.g., marine construction), project planning should ensure no net loss of listed corals. Where natural or anthropogenic impacts do occur, an effective and complete response plan, including appropriate compensatory and site restoration, is executed.

Interim Criterion 10: Predation (Listing Factor C)

Develop a quantitative recovery criterion through research. Based on 5 years of data, a criterion will be established to reduce the impact of predation to a tolerable level appropriate for recovery.

Similar to what was stated above for Interim Criterion 4: Disease, there is a lack of information concerning the abundance of these coral species throughout their ranges and the proportion of colonies and tissue per colony affected by predation. Once a baseline level of predation within each population has been determined, a more measurable criterion for determining whether the threat of predation has been abated can be developed.

IV. RECOVERY PROGRAM

The recovery program for elkhorn and staghorn corals describes the recovery actions that are necessary to achieve the plan's goals, objectives, and criteria. This section of the plan consists of the recovery action narrative and the implementation schedule. The recovery action narrative is organized around each of the main recovery objectives (see II. Recovery Strategy) and describes the specific recovery actions. The implementation schedule states the recovery priority associated with each action, the responsible parties, the estimated cost to complete the action, and the timeframes to complete the actions. NMFS believes that the recovery plan should be a dynamic document that will change over time based on the progress of recovery and the availability of new information. As new information is obtained, additional actions will be identified and incorporated into the plan. As is the case for all recovery plans under the ESA, this plan will be regularly reviewed and the relative success of these actions in protecting elkhorn and staghorn corals assessed. Recovery actions can be changed or added accordingly.

A. Recovery Action Matrix

Table 2 below shows which criterion of Objective 1 or 2 each recovery action addresses. Some recovery actions address multiple criteria across both objectives. Actions are not numbered in order of priority. See the Implementation Schedule for assigned recovery action priorities.

Table 2. Recovery Action Matrix

Action	Objective 1 – Ensure Population Viability	Objective 2 – Eliminate or Sufficiently Abate, Global, Regional, and Local Threats
1 **Implement Outreach and Education Strategies**		All Criteria
2 **Coordinate Recovery Implementation**	All Criteria	All Criteria
3 **Conduct Strategic Research of Elkhorn and Staghorn Coral Biology**	All Criteria	Depensatory Population Effects Threat Interim Criterion 4: Disease Criterion 5: Temperature and Acidification Criterion 7: LBSP
4 **Develop Mapping and Inventory Products**	All Criteria	Depensatory Population Effects Threat Criterion 6: Loss of Recruitment Habitat Interim Criterion 4: Disease

Action	Objective 1 – Ensure Population Viability	Objective 2 – Eliminate or Sufficiently Abate, Global, Regional, and Local Threats
5 **Monitor the Species and Their Environments**	All Criteria	Depensatory Population Effects Threat Criterion 6: Loss of Recruitment Habitat Interim Criterion 4: Disease Interim Criterion 7: LBSP
6 **Conduct Active Population Enhancement**	All Criteria	Depensatory Population Effects Threat Criterion 7: LBSP Criterion 9: Natural and Anthropogenic Abrasion and Breakage Criterion 8: Regulatory Mechanisms
7 **Understand Diseases Affecting Elkhorn and Staghorn Corals**		Interim Criterion 4: Disease
8 **Respond to, Control, and Minimize Effects of Disease Events**		Interim Criterion 4: Disease
9 **Develop and Implement U.S. and International Measures to Reduce Atmospheric CO_2 Concentrations**		Criterion 5: Temperature and Acidification Criterion 8: Regulatory Mechanisms
10 **Develop and Implement Environmentally Sound Mechanisms to Reduce Local Impacts of Temperature Stress**		Criterion 5: Temperature and Acidification
11 **Research and Develop Mechanisms to Enhance Adaptation/Acclimation of Elkhorn and Staghorn Corals to Increases in Climate Stress**		Criterion 5: Temperature and Acidification
12 **Restore, Protect, and Enhance Ecosystem Integrity and Function**		Criterion 6: Loss of Recruitment Habitat Criterion 7: LBSP Criterion 8: Regulatory Mechanisms
13 **Address Sewage Discharges throughout the Species' Ranges**		Criterion 6: Loss of Recruitment Habitat Interim Criterion 7: LBSP

Action	Objective 1 – Ensure Population Viability	Objective 2 – Eliminate or Sufficiently Abate, Global, Regional, and Local Threats
14 **Develop and Implement Effective Watershed/Land Use Management Plans for the Protection of Coral Reefs**		Criterion 6: Loss of Recruitment Habitat Interim Criterion 7: LBSP Criterion 8: Regulatory Mechanisms
15 **Restore and Maintain Mangrove and Seagrass Ecosystem Resources to Buffer Land-Based Influences**		Criterion 6: Loss of Recruitment Habitat Interim Criterion 7: LBSP Criterion 8: Regulatory Mechanisms
16 **Study Organismal Response to Nutrients and Contaminants and Implement Appropriate Remedies**		Criterion 6: LBSP Interim Criteria 4: Disease Criterion 8: Regulatory Mechanisms
17 **Develop and Implement a Pilot Regional Intergovernance Plan**		Criterion 8: Regulatory Mechanisms
18 **Enforce Existing or Develop New Regulations**		Criterion 6: LBSP Criterion 8: Regulatory Mechanisms
19 **Respond to 50 Percent of Known Physical Disturbance Events**		Criterion 9: Natural and Anthropogenic Abrasion and Breakage
20 **Reduce Impacts from Planned Physical Disturbances — No Net Loss from Development Projects**		Criterion 9: Natural and Anthropogenic Abrasion and Breakage
21 **Implement Protective and Preventative Measures to Reduce Physical Impacts**		Criterion 8: Regulatory Mechanisms Criterion 9: Natural and Anthropogenic Abrasion and Breakage
22 **Develop Guidelines for Snail *(Coralliophila abbreviata)* Removal Actions and Undertake Snail Removal Actions in Appropriate Sites**		Interim Criterion 10: Predation
23 **Evaluate Risks and Benefits of Potential Removal Strategies for Other Corallivores**		Interim Criterion 10: Predation

B. Recovery Action Narrative

The following actions are necessary for meeting the criteria and achieving the objectives identified in this plan. The following actions are not listed in order of priority; priority numbers are assigned in the Implementation Schedule (see below). Outreach and education efforts are needed for the abatement of all threats facing these coral species, and recovery coordination at the program level will facilitate coordinating and accomplishing actions and knowing whether the criteria and objectives in this plan have been met. Strategic research of elkhorn and staghorn coral biology is also an overarching action that will provide information for ensuring population viability and also provide more information to fill knowledge gaps related to threats.

The Endangered Species Act requires cost estimates for actions necessary to recover the species. The ART and NMFS derived cost estimates associated with the actions listed below from market research and their own experiences with grants and contracts. In some cases, costs estimates are not known due to the scale of the actions necessary. In addition, because the majority of elkorn and staghorn corals exist outside US jurisdiction, additional actions in foreign nations are likely needed to recover the species. Therefore, the costs approximated here are likely severely underestimated.

ACTION 1: Implement Outreach and Education Strategies

The actions needed to achieve the goal and objectives of this recovery plan have the potential to be expensive and, perhaps, intractable because of the scale of the threats facing elkhorn and staghorn corals (e.g., global climate change, exposure to chemicals and nutrients from non-point sources). The success of this recovery plan is, therefore, dependent upon effective and far-reaching public education and outreach to achieve broad-based reduction of threats and support acroporid conservation. Suggested outreach and education strategies are listed below; however, this is by no means an exhaustive list. Initiation: Immediately. Time: On-going. Cost: Dependent on scale.

a. ***Convey the ecological and economic value of elkhorn and staghorn corals.*** Education and outreach strategies are necessary to convey the ecological and economic value of these two threatened coral species, to impart the scale and severity of the threats facing these coral species, and to provide guidance for recovering these coral species. Such strategies may include: targeting areas for outreach campaigns that are most ready for action; promoting single, simple doable behaviors that lead to changes in the use of land, of fossil fuels, and of coral reef resources; finding more effective communication techniques; and understanding audience barriers to behavior change.

b. ***Build upon existing outreach and education efforts***. Existing outreach and education efforts provide the foundation for engaging more of the public in recovering these coral species and for enacting the recovery actions outlined in this plan. These projects and programs have the necessary existing infrastructure, local partnerships, and recognition upon which to build. Facilitating and expanding collaborations between existing efforts will increase the overall impact and effect of these existing outreach and education efforts.

c. ***Foster stewardship of the coastal ecosystem***. Innovative methods of fostering stewardship of the coastal ecosystem must be identified and implemented to accomplish all of the required recovery actions. This includes fostering stewardship through education, especially for the millions of children who live in the Atlantic/Caribbean; the long-term health of the environment will depend on their interest and ability to protect nature. Additionally, providing lifelong learning opportunities for citizens of all ages, with information and interpretation at a multitude of locations in the Atlantic/Caribbean, is necessary.

d. ***Expand involvement of researchers in interdisciplinary sciences***. There is a need for integrating interdisciplinary science (e.g., medicine, basic sciences, genomics, systems biology, bioinformatics, informatics, etc.) into coral reef research. This can be accomplished by funding interdisciplinary regional assessments, by developing interdisciplinary models that have extended utility, by establishing interdisciplinary science centers at academic institutions throughout the range of these species. Implementation of these actions will leverage funding opportunities and increase the efficacy of existing and future outreach and education efforts by increasing collaborative partnerships.

e. ***Expand education opportunities for graduate scientists***. A new generation of coral scientists can be empowered through the expansion of post-doctoral opportunities and marine science education programs. Addressing this need will expand the available options and viewpoints to address the threats facing threatened elkhorn and staghorn corals.

f. ***Increase involvement of existing regional organizations/alliances.*** There are several existing collaborative governance efforts in the Caribbean which will need to be informed of and involved in the actions included in this recovery plan. Collaboration with and outreach to these organizations will be necessary to increase the international participation in these actions. Recovery of the species at the range-wide scale will be impossible without regional collaborations. Examples of existing collaborations and organizations that can act as recovery partners include the Meso-American Barrier Reef System (MBRS) project and the Caribbean Large Marine Ecosystem Project (CLME) based at the Intergovernmental Oceanographic Commission Sub-Commission for the Caribbean and Adjacent Regions (IOCARIBE) (see also Action 17).

ACTION 2: Coordinate Recovery Implementation

a. ***Ensure coordination and tracking of recovery actions:*** A coordinator is needed to facilitate plan implementation and develop appropriate guidelines for project execution. The coordinator will foster data standardization and coordinate research programs. The coordinator will facilitate international communication and entry of active jurisdictional (domestic and foreign) project reporting into a central data repository. Initiation: Immediately. Duration: On-going. Cost: $150,000 annually.

b. ***Create and maintain a central elkhorn and staghorn coral project/data repository:*** To coordinate and track all on-going recovery actions, a central database is necessary. Initiation: Immediately. Duration: 6 months to develop; on-going maintenance. Cost: $25,000 to develop; maintenance completed by Recovery Coordinator (see Action 2a, above).

Objective 1 – Population Viability

Actions 3 through 6 (below) address Criteria 1 through 3 under Objective 1 – Ensure Population Viability. Criteria and actions under this objective also address the threat of Depensatory Population Effects described in the Threats Assessment.

ACTION 3: Conduct Strategic Research of Elkhorn and Staghorn Coral Biology

Many of the following actions support several criteria listed for Objective 2. Cross-references to these criteria will be made where appropriate in the following discussion.

a. ***Genetic tool development:*** The complex life histories of elkhorn and staghorn corals make genetic tools particularly important for the determination of basic population status. The recent development of microsatellite genetic markers for both elkhorn coral (Baums et al. 2005a) and staghorn coral (Baums et al. 2009) has enabled vastly improved understanding of population connectivity (e.g., Baums et al. 2005b, 2006, 2010) and, importantly, enabled the beginning steps to understand genetic basis for adaptive characteristics that are important to species persistence (Vollmer and Kline 2008). However, improved resolution of genetic markers is needed to efficiently detect adaptive genetic variation and then apply this knowledge to effective population enhancement. A crucial step for this and other recovery needs is the sequencing, compilation, and annotation of an elkhorn or staghorn coral genome (elkhorn coral suggested as first priority). Knowledge of the genome (and then the variation in sequences between individual's functional gene sequences with different characteristics) provides the basis to develop markers with much finer resolution, to more closely diagnose phenotypes, and to develop clinical diagnostics to elucidate, diagnose, and treat pathologies. Some progress may be obtained using information from transcriptomes (sequencing of the gene products being expressed in an individual), and this approach should also be pursued. Finer resolution markers can then be applied to questions of population status (e.g., paternity tests, tests for compatible parental genotypes to enhance fertilization success and larval fitness) and to identify markers for characteristics, such as disease resistance, high temperature and pollutant tolerance, or improved calcification under low pH conditions, that are crucial to species survival in the changing coral reef environment. Similar genetic markers are needed for other components of the coral holobiont (e.g., zooxanthellae, important defensive microbes, etc.). A sequenced and annotated genome for elkhorn and staghorn corals will improve our understanding of the patterns and processes affecting the health of these species and elucidate the biochemical and cellular physiological processes governing health and fitness, which together can assist preservation and restoration activities. This action supports Interim Criterion 4 and Criteria 5 and 7 under Objective 2. Initiation: 2 years. Duration: 3 years (for initial sequencing, assembly, and annotation); On-going (for marker discovery and validation, depending on number of phenotypes). Cost: $3,000,000 (sequencing and annotation); approximately $150,000 per marker.

b. ***Identify determinants of reproduction and recruitment success:*** Determinants of spawning synchrony, fertilization dynamics, parental compatibility, and larval fitness are all poorly understood and are key features of understanding and enhancing reproductive success. Lack of spawning, spawning asynchrony, and developmental abnormalities observed in elkhorn coral in the Florida Keys (Miller et al. pers. obs.) suggest that fundamental processes of reproduction may be compromised in this population. Almost nothing is known of mechanisms of symbiont uptake, larval survivorship (including ecological interactions such as competition), nutritional requirements, and development in elkhorn and staghorn corals. Research to address such basic properties and processes are pre-requisite to developing effective strategies to enhance recruitment and

survivorship of these early life phases (larvae, small settlers, and juveniles). This will include, but is not limited to, identifying cell signaling molecules, developmental programming, hormonal effects, influence of chemical cues for settlement (e.g., by certain types of CCA), and contaminants that may have detrimental effects. Once identified, these parameters can be diagnostic markers in toxicity studies to identify factors that may disrupt normal functioning and tailor management actions to specific causalities. Improved recruitment is a pre-requisite for self-sustaining populations. Elucidating genetic and/or environmental determinants of such processes may allow active enhancement of recovery. Initiation: Immediately. Duration: 3-10 years. Cost: $1,250,000.

c. ***Research cellular physiology and biochemistry:*** Understanding basic coral physiology and cellular processes is important in determining defense mechanisms against pathogens and the coral's tolerance range to all types of environmental stressors including temperature, pH, sedimentation, or pollutants. The ability to successfully, proactively manage for healthy coral reefs depends on the progress made in understanding the causes and responses to adverse effects of physical, biological, and chemical stressors on coral vitality (i.e., coral pathology). Pathology is defined, however, in terms of the "normal" basic physiology. Understanding these basic physiological and cellular mechanisms and pathways is a pre-requisite to defining pathologies accurately and to rapidly advance in managing for acroporid health and resilience. A weak foundation in basic coral biology (e.g., biochemistry, cell biology, genetics, and organismal and cellular physiology) currently hinders progress in the area of acroporid health monitoring and management. This action supports Interim Criterion 4, as well as Criteria 5 and 7, listed under Objective 2. Initiation: Immediately. Duration: 3-10 years. Cost: $1,600,000.

d. ***Research host - symbiont relationships:*** Corals host both symbiotic algae (zooxanthellae) and other microbes that exist in harmony under favorable conditions. However, the interactions between coral-associated microorganisms and their acroporid hosts are poorly understood. Bacteria are a normal part of every organism and are believed to offset potentially harmful microbes by producing antibiotics or simply occupying the available space (Ritchie 2006, Mao-Jones et al. 2010). Elkhorn coral has been shown to harbor potentially beneficial microbes that are replaced by potentially pathogenic bacteria when temperatures increase (Ritchie 2006). The study of temporal and spatial variability in the microbial ecology of elkhorn and staghorn corals may be central to understanding innate coral immunity and changes that corals undergo when stressed, which may lead to disease (Lesser et al. 2007, Mao-Jones et al. 2010). Basic research in symbiosis in elkhorn and staghorn corals will be important in understanding preferential *Symbiodinium* associations, symbiont uptake, cell cycle regulation, and the importance of multi-species partnerships between corals, zooxanthellae, and other microbes. Studies at the cellular and molecular level examining interactions between symbionts and host, such as nutrient exchange, recognition and specificity, and mechanisms driving coral bleaching and disease, are needed (Weis et al. 2008). This type of research will be critical for providing tools and techniques to combat the spread of disease, restore vitality and fitness to elkhorn and staghorn corals, and ultimately, to proactively manage with the goal of healthy reefs. This action supports Interim Criterion 4, as well as Criteria 5 and 7, listed under Objective 2. Initiation: Immediately. Duration: 3-10 years. Cost: $1,250,000.

e. ***Research immunity:*** Environmental factors may alter pathogen physiology inducing a more infectious or pathogenic state or alternatively, environmental conditions may compromise coral defense mechanisms, rendering them more susceptible to infection (Lesser et al. 2007, Mao-Jones et al. 2010). Unfortunately, little is known of coral defense systems (immunology), beyond that they have allorecognition and phagocytic cells. Pathology of coral disease is an issue that continues to challenge scientists and resource managers. Is the disease occurring because of an introduction of a

novel pathogen into the environment, the addition of abiotic factors (e.g., increased iron availability or increased temperature) that induce pathogenesis, or factors causing a decrease in immuno-competence? Resolution of these issues is paramount for effectively understanding and managing coral disease outbreaks. Advancing knowledge of coral immunity and coral epidemiology will require developing an understanding of the coral innate immune system from a biochemical and cellular physiological perspective and translating this information into easy to use, inexpensive, quick, and accessible assays that are functional and quantitative. The first assay adapted to gauge one aspect of coral immunity is a bioassay for anti-microbial peptide isolation and activity (Imcomp-P Assay, Downs et al. 2005a). Ritchie (2006) also monitored levels of antibiotic resistance with microbiology-based assays. Additional aspects of innate immunity have been identified in other cnidaria, and several gene products associated with various types of innate immunity have been found among coral EST[4] library collections. Mining these data will assist in elucidating the various types of immunity manifested in corals and lead to a fuller understanding of their normal functioning and factors that can compromise them (Downs et al. 2005a). This improved understanding will also provide new aspects of genotypic and genetic diversity of different coral populations. This action supports Interim Criterion 4, listed under Objective 2. Initiation: Immediately. Duration: 3-10 years. Cost: $2,500,000.

ACTION 4: Develop Mapping and Inventory Products

a. ***Develop, implement, and maintain a comprehensive species inventory database:*** To facilitate monitoring the status of both species and determining the efficacy of conservation actions, a central comprehensive reporting database must be developed and implemented. The database should include formal (i.e., institutional) and informal (i.e., volunteer monitoring programs) data. This action will identify minimum reporting requirements and be expandable to include more complex data such as coral and symbiont genotypes, environmental parameters, lesion regeneration rates, cellular diagnostics, and/or allozymes. The reporting program will identify geographical information gaps to be targeted for further investigation. Initiation: Immediately. Duration: 6 months to develop; on-going maintenance. Cost: $25,000 to develop; $10,000 annually.

b. ***Develop remote sensing tools:*** To advance the science of monitoring these species' distributions and abundances, new remote sensing tools must be developed. The tools may include satellite, air borne, or ship borne sensors to map location, habitat, and potentially, condition data. The information will be used to supplement *in situ* programs to monitor the status of these species and determine efficacy of conservations actions. Initiation: Immediately. Duration: greater than 5 years. Cost: Unknown.

[4] EST or expressed sequence tag is a short sub-sequence of a transcribed cDNA sequence.

ACTION 5: Monitor the Species and Their Environments

a. ***Develop and implement a range-wide monitoring program:*** Information on population status is needed throughout the Caribbean, Gulf of Mexico, and western Atlantic, both inside and outside U.S. jurisdiction. Additionally, monitoring is required to evaluate the effectiveness of specific actions to abate threats in targeted local areas. Thus, a range-wide monitoring program for elkhorn and staghorn corals needs to be implemented, as substantial variation in population status is known (e.g., eastern Caribbean populations of elkhorn coral are more genotypically diverse and have higher colony density than western Caribbean populations (Baums et al. 2006)). Clearly, this spatial scale requires extensive international cooperation and coordination as the majority of both species lie outside of U.S. territories. Funding and cooperative mechanisms must be identified to enable standardized monitoring throughout this extensive geo-political area. The program will be implemented at two scales —abundance and demographic monitoring. Initiation: Immediately. Duration: On-going. Cost (for all sub-actions): $1,000,000 per year.

   i. *Implement a habitat-stratified random sampling approach for abundance assessment:* To address Recovery Criteriion 1 (population abundance), a habitat-stratified random sampling approach is required throughout these species' ranges. By estimating an absolute colony density and relative abundance (percent cover) within each habitat strata, these estimates can be extrapolated to the entire species range with a quantifiable level of confidence. Miller et al. (2007, 2008b) have executed this type of sampling throughout the Florida Keys, and this program could be used as a model, repeated on a five year interval, to evaluate Criterion 6. To facilitate development of this abundance assessment, high-quality habitat maps must be produced (Action 4b). Existing and potential habitat, based on historic occurrence, needs to be inventoried and characterized. This will require defining what quality of habitat is necessary for recovery, including parameters for the benthos and water column. The characterization will be accomplished using a combination of tools (e.g., remotely-sensed data, in situ observations). Primary focus will be on U.S. jurisdictions, but international habitats are also necessary for recovery.

   ii. *Develop and implement a standardized demographic approach to monitoring:* In order to evaluate Recovery Criteria related to recruitment and genotypic diversity, a standardized demographic approach to monitoring (e.g., Williams et al. 2006), including assessment of recruitment and genotyping of colonies within established plots, should be implemented where feasible (i.e., intermediate density stands). The lesser physical stability of individual staghorn coral colonies makes them less amenable than elkhorn coral to this approach but should be attempted (see Knowlton et al. (1990) for cable tie marking and "stick diagram" approach for tracking tagged colonies). A standardized demographic approach will also maximize the utility of the data for population modeling and projection and provides the best opportunity to determine: 1) the relative importance of various threats (e.g., predation, disease, breakage), and 2) if the prevalence and impact of these threats is changing over time (see Williams and Miller 2012). Permanent plots and marked colonies should be established in all U.S. jurisdictions and multiple additional areas/countries. Additional standardized protocols should be established for thickets, where individual colonies can not be reliably delineated. Thicket protocols might involve standard quadrat/percent cover sampling and/or video mosaics combined with *in situ* prevalence estimates for different types of threats and should also include measurements of the size and spatial extent of the thickets. It may also be appropriate to include low-altitude aerial photographs with ground truthing.

iii. *Evaluate robust reference populations:* Alongside the distributed effort on demographic monitoring of population status, a minimum of three to five robust reference populations will be targeted for each species spread throughout the range for intensive monitoring and research to determine potential demographic, genetic, and/or environmental factors that may account for their robust status. Many aspects of uncertainty delineated in this plan (e.g., predation and disease carrying capacity, sexual and asexual recruitment rates in healthy populations) can be addressed by comparing such robust reference populations with nearby populations which are in a more typical, degraded state. Environmental, toxicological, and ecological parameters should be monitored at these robust reference populations and nearby degraded populations (suggested as part of the demographic monitoring described in Action 5aii, above) to discern the causal differences.

This program may include a coarser-level field protocol to determine these species' statuses at each site through time. The appropriate protocol must be developed; however, it should include both species-focused parameters and environmental parameters.

iv. *Periodically monitor water quality parameters range-wide:* Identify and quantify a suite of contaminants (e.g., pesticides, pharmaceuticals, heavy metals, polycyclic aromatic hydrocarbons, personal care products) to be monitored in both the water column and in sediments. This type of analysis is somewhat expensive and only needs to be done periodically to determine if these compounds are present in the coral reef ecosystem. If found, monitoring for specific compounds should be conducted routinely to track trends. Additionally, quarterly sampling for the more standardized oceanographic parameters, such as nutrients, salinity, chlorophyll a, pH, alkalinity, TOC, DOM, turbidity, etc. should be performed.

b. ***Identify and map genotypes:*** All monitoring and in-water inventory activities should include biopsy sampling to analyze genotypic diversity in the monitored populations. This information should be tracked in an inventory database for these species, as described in Action 4a, above and coordinated with Action 3a (Genetic tool development).

ACTION 6: Conduct Active Population Enhancement

a. ***Develop and implement a comprehensive restocking plan:*** Both listed coral species have a branching morphology and life histories featuring fragmentation that make them amenable to population and/or colony enhancement. Population enhancement may involve a spectrum of activities from stabilizing fragments after physical disturbances, such as groundings or storms, to active culture and restocking of fragments (e.g., Epstein et al. 2001) or larvally derived colonies. Many *in situ* efforts are actively engaged in culturing fragments (particularly staghorn coral, much less so for elkhorn coral) with a high degree of success. However, data gaps remain regarding the success and risks (including health and genetic impacts) of *ex situ* fragment and sexual propagule culture and outplanting. The greatest benefits of outplanting will accrue in areas where environmental conditions are appropriate to support healthy elkhorn and staghorn coral populations.

   i. *Scale up field and land-based nursery culture/restocking efforts:* With growth rates faster than any other Atlantic/Caribbean coral species and asexual fragmentation as the dominant form of reproduction, elkhorn and staghorn corals can be efficiently propagated using land-based and low tech in-water nurseries. While a variety of successful methods have been developed, all generally involve the same concepts. Small fragments (less than 5cm) are collected from the reef and stabilized in a nursery removed from the impacts of the natural environment. Nursery-reared corals can be outplanted to degraded reefs to enhance the genetic diversity and population size of remnant coral populations. These supplemented corals improve local reef structure and function and increase the likelihood of successful sexual reproduction. Nursery-reared fragments of staghorn coral have been observed to spawn within 2 years of outplanting to fore-reef environments in the Florida Keys. Cultured colonies provide a continual source of material for outplanting through successive re-fragmentation. Field nurseries should be established throughout these species' ranges in order to minimize poorly-characterized risks associated with mixing populations (e.g. outbreeding depression). Likewise, land-based nurseries should be established in multiple locations, both to optimize the number and genetic diversity of cultured colonies and to spread the risk from catastrophic events such as hurricanes or major equipment failure. It is crucial that accurate and effective recordkeeping and databases be established to track the genotypes and fate (location of outplants) of cultured corals. Costs will include labor, genetic analysis, boat costs, and materials and should ideally be subcontracted for local efforts. Initiation: Immediately. Duration: On-going. Cost: $10,000,000 annually, although scalable.

   ii. *Develop and implement guidelines/policies for risk management of population restocking:* Risks associated with outplanting of cultured corals to enhance wild populations can be categorized as 1) deleterious genetic consequences for the wild population, or 2) potential health impacts to the wild population (e.g., via introduction of a transmissible disease condition). These concerns must be addressed as a component of effective restocking from either land-based or field-based culture efforts. Though genetic risks have been addressed for various other taxa (e.g. FWC Genetic Policy for the Release of Finfishes in Florida), ecological and genetic characteristics of corals (e.g., regular and natural occurrence of hybrids, potentially as a key evolutionary feature (Veron 1995, Vollmer and Palumbi 2002)) imply differing genetic risks. Baums (2008) outlines what is known and specific research needs to reduce uncertainty and manage risks associated with genetic consequences of coral restocking. Uncertainties regarding health impacts are even greater. Results from disease research (articulated elsewhere in this plan) should be utilized to better estimate and manage such risks. "Best practices" should be applied, such as testing

exposures first in laboratory conditions, and perhaps next in "field quarantine" areas (e.g. distant from high abundances of live coral). These uncertainties represent a basis for a cautious approach and dictate specific research actions, but should not paralyze cautious experimental evaluation and progressive implementation of restocking efforts given the threatened state of these species. An ongoing effort by experts in coral health and coral genetics is needed to formulate and refine comprehensive risk management strategies as knowledge improves. Initiation: Immediately. Duration: 3 years. Cost: $500,000.

b. ***Stabilize/reattach both storm-generated and anthropogenic fragments:*** (Also addresses Criterion 9: Natural and Anthropogenic Abrasion and Breakage) Though fragmentation is a natural and, at times, effective means of reproduction in elkhorn and staghorn corals, it also imposes a cost as loose fragments are vulnerable to abrasion and transport to unsuitable habitat. While loose fragments often survive the direct physical breakage, ultimate survival depends on a fragment landing in a stable position, on a suitable hard substrate free of macroalgae and turf algae, away from predators, and on a reef not subject to high turbidity and sedimentation. Easy and effective methods of proactive stabilization (e.g., using cable ties, Portland cement, or epoxy) have been demonstrated to significantly enhance the performance of small elkhorn and staghorn coral fragments (Williams and Miller 2010). Even simply moving fragments from unsuitable habitat (e.g. sand) and wedging them into reef crevices may be effective in enhancing recruitment. Proactive stabilization of both anthropogenic and naturally-produced fragments should be implemented in appropriate contexts (e.g., areas where they are prone to migrate downwards into sand pockets or times when probability of subsequent disturbance is high). Funding in the form of labor, materials, and boat costs will be required for response actions. Initiation: Immediately. Duration: On-going. Cost: $2,000,000 annually, although scalable.

c. ***Enhance genotypic diversity in known genotypically depauperate populations:*** Certain populations, particularly of elkhorn coral, have been documented as comprised of single or very few genetic individuals (Baums et al. 2006). Because these species are obligate outcrossers (i.e., they cannot self-fertilize) and spawned gametes are only viable for a couple of hours, such populations have negligible chance of effective fertilization (so-called Allee effect). Hence, there is negligible larval production despite hefty physiological investment in gamete production. Transplanting fragments of compatible genotypes from nearby populations or nurseries within such depauperate stands should enable successful larval production. Pilot spawning observations (to ensure synchrony) and larval crossing experiments between the target population and candidate "import" genotypes should be a preliminary step, as preliminary observations in Florida Keys populations suggest that not all genotypes are equally compatible in terms of spawning synchrony or larval fitness (Miller and Baums pers. comm.). Alternatively, "fragments of opportunity" from nearby diverse populations might be used for transplants. Initiation: Immediately. Duration: On-going. Cost: $150,000 first year; $500,000 annually, although scalable.

d. ***Develop ex situ conservation of corals and related organisms:*** Given the likelihood of worsening conditions (e.g., estimates for an additional 2°C warming already committed) for elkhorn and staghorn corals in Atlantic/Caribbean reef environments over the next decades, there is also a need to pursue strategies for *ex situ* conservation. Approaches might include the careful maintenance of captive populations as well as the development of effective cryo-preservation and storage for elkhorn and staghorn coral gametes in genome banks or tissue micropropagation (Vizel et al. 2011). Laboratory propagation via fragmentation is fairly routine for staghorn coral, but less so for elkhorn coral. Captive populations should be optimized to supply research stocks for experimental needs as they will provide standardized material for genetic and physiological research and relieve collection

stress on wild populations. Best husbandry practices should be documented. Successful *ex situ* strategies for these corals will be more complicated than for standard vertebrates in that zooxanthellae and other microbial symbionts are specialized and crucial for holobiont fitness. Important components of such a strategy would be a comprehensive tracking system for captive and "banked" material.

Novel *ex situ* conservation techniques, such as genetic banks using frozen samples, reflect a new and major type of preservation that can be added to conventional archives to include gametes, embryos, somatic and stem cells, and DNA. Genome repositories can be used to keep genetic material frozen but alive for hundreds of years in liquid nitrogen, maintain large samples of a gene pool, and increase genetic diversity within an ecosystem through the use of thawed samples to 'seed' shrinking populations. Research is needed in all of these areas of potential utilization and application of banked genomic material. Coral sperm has been successfully cryopreserved (Hagedorn et al. 2006a; Hagedorn et al. 2006b), and three genome repositories worldwide now hold cryopreserved sperm from elkhorn coral (Hagedorn et al. unpublished data). A comprehensive strategy for genome banking in these species should be developed (Global Coral Repository, Downs et al. unpublished). Initiation: Immediately. Duration: On-going. Cost: Unknown.

e. ***Enhance survival of recruits:*** (Also addresses Interim Criterion 7: Land-Based Sources of Pollution) Even when the hurdles of fertilization, larval development, and settlement are surmounted, the post-settlement survivorship of elkhorn and staghorn coral larvae appears to be extremely low. Even the large fragment propagules of elkhorn and staghorn coral can display very low rates of survivorship. Proactive stabilization of loose fragments by simple means, such as epoxy or cable ties, and co-culture with herbivorous snails (successfully demonstrated in Japan with Pacific *Acropora* spp., see Edwards and Gomez 2007), can improve their performance and should be undertaken in appropriate circumstances (see other sections). Local manipulations such as enhancing substrate quality, enhancing settlement cues, or protection from predators should be explored. Long term improvement in survivorship of larval recruits likely involves community and ecosystem level improvements to restore trophic balance (e.g. marine reserves and/or re-establishment of *Diadema*) and improve water and substrate quality, as described in other areas of this plan. Initiation: Immediately. Duration: On-going. Cost: Unknown.

f. ***Conduct applied population enhancement research***

   i. *Land-based rearing of corals:* Currently, the risks and benefits associated with using land-based cultured material for wild re-stocking are very poorly understood. It is reasonable to assume that the risks posed in wild population restocking would be greater for corals cultured in land-based, closed systems than for corals cultured in field nurseries (open system land-based culture might be intermediate). This presumption is based on the fundamental environmental differences between aquaria and ocean conditions that are expected to drive changes in the coral itself and/or in its microbial flora during culture. However, if the corals and associated microbial communities are able to acclimate to aquaria, they would presumably also be able to re-acclimate to open ocean conditions. However, these presumptions need to be tested so that risks can be evaluated and managed in any activities restocking wild populations from land-based culture sources. Research for optimizing methods and managing risks associated with land-based rearing of elkhorn and staghorn corals is needed both for the effective implementation of *ex situ* conservation strategies and for pursuing effective strategies for population restocking from sexual propagation. Immediately. Duration: On-going. Cost: $500,000 per facility.

ii. *Larval settlement, recruitment, grow-out, and restocking:* Active intervention in sexual propagation is important to enhance larval production from wild populations by overcoming Allee effects and, likely, by providing more conducive environments for larval development. Elkhorn and staghorn corals appear to be particularly sensitive to warm temperatures during the fertilization and larval stages (Negri et al. 2007, Randall and Szmant 2009). Some progress has been made in effective larval culture and settlement (Petersen et al. 2008), but much remains to be learned in terms of enhancing settlement rates and survivorship/growth of settlers both in the laboratory and, particularly, after outplanting. Outplanting survivorship can likely be optimized via a short grow-out phase in the laboratory to attain a size that will reduce mortality from competition and incidental predation, but this needs to be demonstrated. Grow-out conditions need to be optimized, perhaps incorporating co-culture with snails as has been effective in Japan (Omori et al. 2008). Initiation: Immediately. Duration: On-going. Cost: $300,000 per facility.

Objective 2 – Eliminate or Sufficiently Abate, Global, Regional, and Local Threats

Interim Criterion 4: Disease

ACTION 7: Understand Diseases Affecting Elkhorn and Staghorn Corals

Control and mitigation of diseases affecting elkhorn and staghorn corals is impeded because the factors and their interactions (host, agent(s), environment) that determine disease occurrence in these corals are poorly understood (Richardson 1999). Very little is known about the etiology of Caribbean *Acropora* diseases. There is speculation that many coral diseases are the result of opportunistic or polymicrobial infections that are initiated once the coral host immunity has been compromised (Lesser et al. 2007, Work et al. 2008). Many marine bacteria are resistant to cultivation, thus inhibiting a definitive identification and the testing of pure strains as disease-causing agents in healthy corals (Ritchie et al. 2001). Though some information is emerging about the relationship between disease and temperature induced bleaching, scientists are only beginning to explore disease relationships with other physical environmental stresses (e.g., pH, salinity); and uncovering relationships between coral disease and environmental degradation (e.g., pollutants) is at the earliest stages (Jaap & Wheaton 1975, Ostrander et al. 2000, Downs et al. 2010). Because of the complex physical, chemical, and biological interactions affecting coral health, understanding these factors and interactions will require an investigative approach, drawing on many types of information being proposed in this Recovery Plan and elsewhere to develop quantitative comparisons among groups and various factors. A mechanistic understanding of modes of action, susceptibility differences among species, interactions between chemical and environmental variables (e.g., temperature, salinity, light), and tools that allow detection of exposures and effects will enable causal and risk analyses to be used for coral reef assessments (Hahn and Stegeman 1999, Downs et al. 2005b).

Practical approaches developed from the theory of epidemiology (Thursfield 2007), integrated environmental assessment, causal analysis, and risk assessment are needed to provide a quantitative basis for informed management decisions (Downs et al. 2005b, 2011, Suter 2006). These methods offer a forensics investigative approach to understanding the complexities of disease by blending pathology and epidemiology (i.e., biological assessment and causal analyses) with risk assessment (i.e., risk models that link alternative decisions to future conditions) to provide a systematic means to better identify causal factors and their path from source to impairment.

Three inter-related research priorities to determine risk factors and their relative contribution to *Acropora* disease are:

1. ***Condition assessment:*** The first step is to choose specific health indicators (e.g., percent coral cover, genetic diversity, lesion regeneration, physiological diagnostic markers, reproductive viability) that can be easily measured in field monitoring efforts to be able to detect change (i.e., condition assessment) (Downs et al. 2005b, Cormier and Suter 2008) in coral health at the population and individual organism levels. Surveys are conducted to establish normal levels for the relevant health indicators so changes in the coral's condition (possibly leading to impairment) can be detected (see Action 5: Monitor the Species and Their Environments). Similar to biological monitoring, monitoring of the chemical (e.g., water quality, toxicants) and physical (e.g., temperature, water flow, turbidity, sedimentation) nature of the environment is performed to detect background levels and changes that might be associated with alterations in biological condition.

2. ***Stressor identification and causal pathway assessment:*** There are numerous methods that can be used to determine causality such as exposure-response relationships, pathology, biochemistry, cellular physiology, and mechanistic models. Whichever method(s) is used, it must be able to identify putative causative agents, identify the links in the cause-effect chain, recognize the level of uncertainty associated with each link, and discriminate among possible causes and the relative contribution of each in inducing the observed effect. As these relationships and interactions are explored, it is vital to also establish that the interactions are supported along a hierarchical biological chain in order to determine mechanisms of action. Possible causes of harm to coral health are inferred by evaluating how the chemical, physical, and biological environments interact to affect the health of organisms within the particular context (Wobeser 1994, Cormier 2006, Suter 2006, Thursfield 2007).
3. ***Ecological risk assessment:*** An ecological risk assessment is a tool that can help managers generate sound information as a basis for management action(s) toward a particular activity or problem. Relative risk factors are assigned to the potential causes of impairment, and management alternatives, including no action, are then developed based on the risk assessment. It is a powerful and cost-effective tool in determining the probability of a risk (or threat) to the resource (i.e., corals) by a stressor (activity or specific pollutant(s)) when funds, expertise, and time are limited. This tool does not require knowledge of the mechanism of the impairment to coral (e.g., increased disease, population decline, loss of reproductive fitness), but if the concentration of pollutant or extent of activity under question (exposure characterization) can be shown to pose a credible threat to the biological integrity of the resource (effect characterization), it can be used as the basis for a management action.

For all three parts of this action, Initiation: Immediately. Duration: Estimate 2-5 years for initial assessment, then on-going. Cost: $500,000 to $2,000,000 per watershed per year but highly variable and dependent on management actions or need for greater certainty.

ACTION 8: Respond to, Control, and Minimize Effects of Disease Events

a. ***Identify and protect apparently resistant and/or resilient areas:*** Surveillance and research efforts are needed to fill gaps in knowledge of disease resistance and resilience including genetics and cellular physiology. Using existing monitoring programs to identify the most resilient areas for elkhorn and staghorn coral stands in various jurisdictions, diagnostics of more tolerant individuals can be performed, and other proactive approaches can be employed to enhance resistance, acclimation, and eventual adaptation of individuals. Working with the local jurisdictions will provide the most comprehensive level of protection and conservation in a practical and enforceable manner. Initiation: Immediately. Duration: 3-5 years. Cost: $500,000 per year.

b. ***Develop capacity to respond to disease events:*** The Coral Disease and Health Consortium (CDHC) has established protocols for responding to coral disease outbreaks by collecting data and samples (Woodley et al. 2002, 2008), and these protocols should be implemented using local and regional capabilities. One way to facilitate this action is to incorporate disease reporting into local BleachWatch Programs' (http://isurus.mote.org/Keys/bleaching.phtml) protocols to identify coral disease outbreaks and provide an early warning system for detecting diseased elkhorn and staghorn corals. This field response component needs to be supported by having laboratories with diagnostic testing capabilities available and poised to conduct analyses. See also Actions 22 and 23 under Interim Criterion 10. Initiation: Immediately. Duration: On-going. Cost: $750,000 per year.

c. ***Develop and test effective mitigation approaches:*** Even in the absence of perfect mechanistic understanding of disease etiology, mitigative approaches must be developed to minimize the impact of disease on affected colonies. Procedures have been developed for physical removal of black band disease (BBD) from some species of corals (Hudson 2000). BBD has not been reported in elkhorn or staghorn coral, so alternative approaches must be developed and evaluated for disease affecting these two coral species. Such mitigative actions could range from simple, such as actively removing diseased portions of the colony by fragmentation and re-attaching the apparently healthy portions of branches from diseased colonies to appropriate substrates, to the more sophisticated, such as using probiotics and phage therapy for treating coral disease (Rosenberg et al. 2007, Efrony et al. 2009, Teplitski and Ritchie 2009). Initiation: Immediately. Duration: 5-10 years. Cost: $500,000 per year.

d. ***Take mitigative action:*** As knowledge of specific risk factors contributing to coral health declines become better defined and as understanding of how these factors affect coral health is discerned, mitigation actions can be crafted and implemented to address specific local situations. These actions may include such measures as quarantine, controlled or timed releases of wastewater or pollutants, or maximal limits for visitors at a given reef during a specific time frame, which will be dictated by the specific stressor(s) affecting the area. Initiation: Immediately. Duration: On-going. Cost: Unknown.

Criterion 5: Local and Global Impacts of Rising Ocean Temperature and Acidification

ACTION 9: Develop and Implement U.S. and International Measures to Reduce Atmospheric CO_2 Concentrations

The predicted increases in ocean warming and acidification associated with increases in atmospheric CO_2 concentrations are expected to increase the impacts on elkhorn and staghorn coral health and populations. In the early 1980s, the frequency of thermal stress events began to exceed the ability of these coral species to recover from bleaching and disease impacts, in some cases decreasing coral reef integrity. Caribbean maximum monthly temperatures over the past decade (2001-2010) were over 0.5°C higher than those recorded in the 1970s. The open ocean aragonite saturation state in the Caribbean has decreased from approximately 4.0, optimal for coral growth, to less than 3.8 as CO_2 levels increased from below 340 ppm in the 1970s to 400 ppm in 2013. Projected increases in sea surface temperature and acidification over this century are widely expected to pose continued threats to coral reefs. Actions would need to be taken both domestically and internationally to maintain thermal and aragonite saturation state conditions across the geographic range of these two species at levels needed for recovery.

Addressing atmospheric CO_2 concentration levels cannot be done through local actions alone and will require concerted action on the part of the global community. International agreements and domestic measures and regulations are likely to be required to meet this goal (Also addresses Objective 2: Criterion 8 —Regulatory Mechanisms). Initiation: Immediately. Duration: On-going. Cost: Unknown.

ACTION 10: Develop and Implement Environmentally Sound Mechanisms to Reduce Local Impacts of Temperature Stress

While emissions reductions are needed for a long-term solution to problems driven by climate change, geo-engineering solutions to both increase surface ocean alkalinity and reduce thermal stress may provide short-term resources to combat the local effects of harmfully elevated ocean temperatures and decreased aragonite saturation at a limited set of specific reefs. However, local mitigation efforts to increase alkalinity and reduce bleaching should be critically evaluated in terms of risks and benefits. Potential experimental innovations to reduce bleaching include shading of strategic, high-value populations or reefs (high light exposure interacts with warm water to trigger mass bleaching events), or pumping of cooler subsurface or chilled waters onto reef habitats. To minimize the potential for negative ecosystem impacts (e.g., from shading or potential nutrient enrichment from sub-surface waters), such engineering measures could be applied over limited time frames when risks of bleaching were particularly high. Initiation: Immediately. Duration: On-going. Cost: Unknown.

ACTION 11: Research and Develop Mechanisms to Enhance Adaptation/Acclimation of Elkhorn and Staghorn Corals to Increases in Climate Stress

There is consensus that in a world that is 2°C warmer than preindustrial levels, the risk of coral extinction is more likely (Carpenter et al. 2008). There is a need to research and test biological or physiological enhancements that might improve these species' resistance to climate changes (both the cnidarian host and symbionts). These may include relatively less sophisticated approaches such as applying selection in culture/restocking efforts for traits such as disease or toxin resistance, and/or thermal or pH tolerance. More sophisticated approaches might also be explored. It is important in any bio/physiological enhancement to be mindful of potential physiological tradeoffs of adaptive traits (e.g.,

thermally tolerant genotypes might display lesser growth or reproductive potential). Initiation: Immediately. Duration: 5 years. Cost: Unknown.

Criterion 6: Loss of Recruitment Habitat

ACTION 12: Restore, Protect, and Enhance Ecosystem Integrity and Function

Several types of actions may enhance larval settlement rates and growth to larger colonies by improving the quantity and quality of available benthic habitat.

a. ***Enforce and improve existing fishing regulations:*** Because Atlantic/Caribbean marine ecosystems have been substantially disrupted by overexploitation of reef fishes (Jackson 2008), protecting fish populations through enforcement of existing fishing regulations, development of improved regulations using an ecosystem approach, and strategic implementation of marine reserves may provide an environment more conducive to successful settlement and recruitment of elkhorn and staghorn corals. Implementing such regulatory steps will require an effective education and outreach program to improve public understanding of and support for healthy marine ecosystems that may, in turn, enhance repopulation by these threatened coral species. This action also addresses Criterion 8: Regulatory Mechanisms. Initiation: Immediately. Duration: On-going. Cost: Unknown.

b. **Implement *Diadema antillarum* restocking**: The massive die-off of *Diadema antillarum* in the early 1980's contributed to a phase shift from coral to macro-algal dominated reefs. Return of this keystone species has been slow over the last 25 years, but in areas where urchin density has recovered to near pre-mortality levels, increases in coral recruitment have been observed (Edmunds and Carpenter 2001, Carpenter and Edmunds 2006). Thus, restocking of cultured urchins may be a means of restoring habitat conditions suitable for recruitment of elkhorn and staghorn corals, but pilot studies are needed to evaluate effectiveness. Initiation: Immediately. Duration: On-going. Cost: $5,000,000

c. ***Implement effective MPAs:*** MPAs regulate destructive and deleterious activities through restrictive use. For instance, they can improve overall ecosystem function by regulating extractive activities such as fishing that result in system imbalance or anchoring which can result in physical damage to habitat. For instance, Mumby et al. (2007b) found that reduced fishing pressure led to a trophic cascade that resulted in enhanced coral recruitment inside a Bahamian MPA. The efficacy of MPAs is affected by the size and location of the protected areas as well as the ability to effectively prevent unauthorized or destructive activities. Existing MPAs must be enforced to their full extent and evaluated for effectiveness. Additional MPAs may be appropriate and sited throughout the species ranges. This action also addresses Interim Criterion 7: Nutrients, sediments and contaminants (Land-Based Sources of Pollution), Criterion 8: Regulatory Mechanisms, and Criterion 9: Natural and Anthropogenic Abrasion and Breakage. Initiation: Immediately. Duration: On-going. Cost: Unknown.

d. ***Conduct research on other invertebrates:*** Grazing by herbivorous invertebrates other than *Diadema*, such as gastropods and crabs, may have positive (Coen 1986) or negative effects on coral recruitment and merits further research (Klumpp and Pulfrich 1989). Rhyne et al. (2009) found 6 million invertebrate grazers were collected for the ornamental and aquaria trade from the Florida Keys in 2007, the effect of which on coral recruitment is unknown. Initiation: Immediately. Duration: 5 years. Cost: $100,000.

e. ***Conduct research on Palythoa caribaeorum:*** The zoanthid *Palythoa caribaeorum* is common in many shallow reef environments and is an aggressive competitor than can overgrow most sessile reef invertebrates (Suchanek and Green 1981) and pre-empt space in areas that formerly supported stands of elkhorn coral. *Palythoa* dominance may represent an alternate stable state (Knowlton

1992) to elkhorn coral dominance in shallow reef crest habitats, and dynamics of *Palythoa* is a topic that merits investigation and the possibility of controlled removals. Initiation: Immediately. Duration: 5 years. Cost: $100,000.

Interim
Criterion 7: Nutrients, Sediments, and Contaminants (Land-Based Sources of Pollution

ACTION 13: Address Sewage Discharges Throughout the Species' Ranges

As discussed in the Threats Assessment section, sewage is the source of some disease agents (e.g., Krediet et al. 2009), nutrients, and contaminants.

a. ***Identify, determine, and implement appropriate mechanisms for sewage disposal in the U.S. and Caribbean***: Because site-specific circumstances will differ (e.g., soil characteristics, slope of land, population density), site-specific planning is required to evaluate the best sewage disposal options for any locale. Planning must take into account collection, treatment, characteristics of the receiving water body (depth, currents, biological community), and economics. Direct discharge of pollutants to surface waters is the least desirable disposal option because it results in a direct exposure of organisms to pollutants in the discharge. Shallow or deep well discharges, depending on the geologic characteristics of the area, reduce the risk for exposure of shallow water organisms to discharged pollutants because of dilution with groundwater before potential pollutants are brought to the surface. The theory behind reuse of wastewater is that when treated wastewater is applied to upland sites, nutrients can be removed by vegetation. Vegetation can act to "polish" wastewater effluent. However, care must be taken with design and implementation of reuse systems. For instance, if applied to inappropriate areas (e.g., hillside, rocky substrate), the reuse water could rapidly enter surface waters with little or no "polishing." Nutrients inadvertently discharged to waters could result in plankton blooms and other undesirable effects. There is also some evidence that reuse of treated wastewater may cause a long-term buildup of many toxic chemicals in the treated area (Zoller 2008). Site specific evaluations and pilot studies should be performed to evaluate the benefits of reuse options. Initiation: Immediately. Duration: On-going. Cost: $10,000,000 - $20,000,000 (depending on the size of the facility and the extent of upgrades).

b. ***Implement tertiary treatment of wastewater in U.S. jurisdiction***: Advanced wastewater treatment (AWT) results in an effluent with reduced suspended solids (5 mg/l) and reduced nutrients (nitrogen (3 mg/l) and phosphorus (1 mg/l)). The nutrient concentration in AWT effluent is similar to that of drinking water. Because the impacts of nutrient addition to aquatic ecosystems are well known and documented, and nutrient removal is practical, implementation of AWT standards for all treatment systems in U.S. jurisdictions in the Atlantic/Caribbean basin, particularly those within watersheds of coral ecosystems, is warranted. This can be accomplished through regulation (Also addresses Criterion 8: Regulatory Mechanisms). The cost of implementing AWT currently does not factor in the cost to the ecosystem of less environmentally safe treatment options. Adding the cost to the ecosystem in cost-benefit calculations of sewage treatment options should be required. In areas where central collection and AWT treatment are not practical, NMFS supports on-site treatment systems built to best available technology standards. Examples include an aerobic treatment system with shallow well or the use of plant beds or wetland cells for nutrient uptake. Use of plants for nutrient uptake will require disposal of plant biomass. Experimental use of plant beds with LECA (light expanded clay aggregate) substrate demonstrated that the aggregate must be replaced approximately every ten years due to saturation of phosphate binding sites (Anderson et al. 1998, Ayres Associates 2000). This action is aimed only at the U.S. at this time because the existing level of wastewater treatment is secondary, whereas in most other nations in the Caribbean, wastewater treatment is not yet at this level. Initiation: Immediately. Duration: approximately 2-3 years. Cost:

Varies, e.g., $14.8 million (for a new 160,000 gallons per day (gpd) sequential batch reactor treatment plant for 1000 equivalent dwelling units (homes), including plant and collection system).

ACTION 14: Develop and Implement Effective Watershed/Land Use Management Plans for the Protection of Coral Reefs

Coastal construction practices can result in sediment and other pollutant loads that have major impacts on nearby water. For example, road building projects on islands with significant slope can create massive turbidity plumes including contaminants via stormwater runoff that can detrimentally impact exposed benthic and nektonic organisms. Incorporation of BMPs, including newly developed "Green" standards, in new project plans can eliminate many of the potentially detrimental effects of coastal construction or other land use projects (e.g., PBS&J 2008). Examples of BMPs include the use of sediment and erosion controls, such as sediment traps, retention ponds, vegetative swales, hay bales, sediment fences, and dechannelization. These BMPs could be instituted via regulations (Also Criterion 8: Regulatory Mechanisms). BMPs can reduce the sediment loading in runoff water and protect adjacent marine systems from being smothered with sediments and exposed to other pollutants. Retrofitting BMPs on existing infrastructure can eliminate major sources of pollution through relatively simple actions. For example, unpaved roads on steep slopes are a particularly significant source of sediments to adjacent waters downslope. Paving roads on slopes and incorporating roadside swales and/or retention ponds to filter and trap any pollutants mobilized by rain events can eliminate or significantly reduce that source of pollution. Initiation: Immediately. Duration: On-going. Cost: Dependent on scale.

ACTION 15: Restore and Maintain Mangrove and Seagrass Ecosystem Resources to Buffer Land-based Influences

The communities of the coastal ecosystem are physically and biologically connected. Impacts to one component can significantly influence other components. Mangroves and seagrass meadows, along with providing nursery habitat for reef species and export of organic matter to adjacent waters, stabilize shorelines and reduce sediment and nutrient loading to adjacent coral reef communities. Dissolved organic matter produced by mangroves and seagrasses has also been shown to be protective to corals by absorbing harmful ultraviolet light (Stabenau et al. 2004, Scully et al. 2004, Shank et al. unpub. data). Thus, future activities must recognize the functional linkage between community types, and existing laws and regulations that protect adjacent communities such as mangroves and seagrasses from damage must be strictly enforced (Also addresses Criterion 8: Regulatory Mechanisms). However, because of the historical loss of much acreage, coastal restoration and land acquisition projects should be implemented to increase buffering of land-based influence to protect ecosystem health. Initiation: Immediately. Duration: On-going. Cost: Dependent on scale.

ACTION 16: Study Organismal Response to Nutrients and Contaminants and Implement Appropriate Remedies

The growing human population in coastal watersheds, as well as the increased sophistication of the chemical and pharmaceutical industries, has resulted in a concurrent increase in discharges of chemical pollutants to coastal waters (Kennish 1997). Organisms living in coastal waters have been exposed to a plethora of new drugs, pesticides, bottom paints, and other chemicals that they never before experienced.

a. ***Conduct controlled exposure experiments:*** Sublethal and long-term effects of exposure need to be investigated through controlled exposure experiments with individual compounds and the

synergistic effects of multiple compounds. Initiation: Immediately. Duration: approximately 6 months per chemical. Cost: $300,000-$500,000 per chemical (based on industry pricing for EPA protocols including bioassays, passive sampling, and toxicity testing (Mueller et al. 2007)).

b. ***Develop biocriteria:*** Data from the research above can be used to define the tolerances of selected organisms (corals) to pollutants; once tolerances are known, biocriteria can be established. Biocriteria can be numerical water quality standards that define the suite of environmental conditions required for the life and reproduction of target organisms (i.e., elkhorn and staghorn corals) (Also addresses Criterion 8: Regulatory Mechanisms). Initiation: Immediately. Duration: approximately 6 months per chemical. Cost: Likely cost shared with Action 16a.

Criterion 8: Regulatory Mechanisms

ACTION 17: Develop and Implement a Pilot Regional Intergovernance Plan

Because elkhorn and staghorn corals are distributed throughout the entire Atlantic/Caribbean basin and face similar global and regional threats, uniform policies and regulations across their entire geographic ranges are necessary for their recovery. As discussed in the Threats Assessment and Conservation Measures sections, the implementation of a patchwork of laws, regulations, policies, and management actions has been largely ineffective in assuring the survival of these species. Development of a regional intergovernance scheme that crosses political boundaries could achieve this goal. Because this recovery plan is organized under U.S. law, the U.S. Caribbean (including Puerto Rico and the USVI) will be a target region for development of a pilot regional intergovernance plan.

a. ***Develop a pilot regional intergovernance plan in the U.S. Caribbean:*** The first step is to define site-specific threats to the corals, including human uses, and display them in GIS formats. This mapping approach is a visual method of illuminating threats, suggesting solutions, and engaging stakeholders. Once this step has been completed, several ocean governance projects in the Caribbean may serve as examples for further development of the pilot regional intergovernance plan in the U.S. Caribbean to coordinate various policies and management actions so that there is a uniform approach to coral conservation. The Meso-American Barrier Reef System (MBRS) project used a regional governance approach to define biophysical characteristics and human use patterns, and identify potential conservation management measures within a four-country region of the western Caribbean. At an even larger scale, the Caribbean Large Marine Ecosystem Project (CLME) based at the Intergovernmental Oceanographic Commission Sub-Commission for the Caribbean and Adjacent Regions (IOCARIBE), Cartagena, Colombia is an excellent example of a multilevel governance network linking regional intergovernmental initiatives together and with the Caribbean Sea Initiative of the Association of Caribbean States. Initiation: Immediately. Duration: On-going. Cost: Unknown.

b. ***Develop a strategic marine spatial plan and zoning plan:*** A key component of the pilot intergovernance plan includes strategic marine spatial planning and ocean zoning to protect the connectivity of coral populations. This also includes appropriate land-use practices. Where changes in land use are needed to abate or prevent the threat from LBSP, land acquisition may be an effective conservation tool. Marine spatial planning and ocean zoning can help address the problems of spatial mismatches (see Inadequacy of Existing Regulatory Mechanisms) (Carollo et al. 2009, Crowder et al. 2006). Although property rights and management arrangements in the sea differ from those on land, spatial planning can be initiated with cooperation among federal, state/territorial, and local authorities. Marine zoning adds an important spatial dimension by defining areas within which compatible activities can occur without replacing existing fishing regulations or requirements for oil and gas permits.

   Key elements of successful marine zoning include: 1) locating and designating zones based on the underlying topography, oceanography, and distribution of biotic communities, 2) designing systems of permits, licenses, and use rules within each zone, 3) establishing compliance mechanisms, and 4) creating programs to monitor, review, and adapt the zoning system. Not only does comprehensive marine zoning directly address fragmentation and spatial mismatches, marine zoning also facilitates efforts to adjust governance to the rhythms of human institutions and the dynamics of spatially bounded ecosystems. Initiation: Immediately. Duration: On-going. Cost: Unknown.

ACTION 18: Enforce Existing or Develop New Regulations

a. ***Enhance and Maximize Enforcement of existing regulations:*** There are several existing regulations that can assist in the recovery of the listed corals if implemented specifically for protection of coral reefs . For example, sediments, nutrients, and contaminants are considered "pollutants" under the CWA, and according to EPA are the most common causes of impaired waters. However, discharges of waters containing nutrients, sediments, and contaminants at levels that affect the corals (i.e., cause biological impairment) and their habitat are unregulated under the CWA in many locations due partly to the lack of knowledge of levels that are harmful to corals (see Action 16). Application of CWA to coral reef environments would greatly reduce impact of LBSP on the species. Also, many laws exist within the state and local jurisdictions that prohibit physical impacts to reefs. However, inadequate budgets and personnel resources often results in infrequent enforcement of the regulations. Additional enforcement officers are necessary to implement existing regulations. Initiation: Immediately. Duration: On-going. Cost: $100,000 per officer for physical impact enforcement. Total cost of this action is dependent on scale. Some areas will need more/fewer officers depending on enforcement needs.

b. ***Adopt new regulations:*** Additionally, new regulations described under the following actions are necessary to abate particular threats affecting these species:

- Action 9: Develop and Implement U.S. and International Measures to Reduce Atmospheric CO_2 Concentrations
- Action 12: Restore, Protect, and Enhance Ecosystem Integrity and Function
    - Action 12a: Enforce and improve existing fishing regulations
    - Action 12b: Implement effective MPAs
- Action 13: Address Sewage Discharges Throughout the Species' Ranges
    - Action 13c: Implement tertiary treatment of all wastewater in U.S. jurisdiction
- Action 14: Develop and Implement Effective Watershed/Land Use Management Plans for the Protection of Coral Reefs
- Action 15: Restore and Maintain Mangrove and Seagrass Ecosystem Resources to Buffer Coral Reefs from Land-Based Influences
- Action 16: Study Organismal Response to Nutrients and Contaminants and Implement Appropriate Remedies
- Action 21: Implement Protective and Preventative Measures to Reduce Physical Impacts
    - Action 21a: Reduce impacts of fishing gear/techniques.
    - Action 21b: Improve management of salvage operations to prevent impacts.

These are addressed in the individual threat based actions and cross-referenced to addressing Criterion 8: Regulatory Mechanisms. Initiation: Immediately. Duration: On-going. Cost: Unknown.

Criterion 9: Natural and Anthropogenic Abrasion and Breakage

ACTION 19: Respond to 50 percent of known physical disturbance events

a. ***Develop and implement response mechanism for physical impact events:*** Physical impacts from hurricanes, vessel groundings, anchors, and marine debris are threats to coral reef health and integrity. These impacts present a direct disturbance to the coral environment that can completely alter a reef's structure and function. Coral reefs in the U.S. Atlantic/Caribbean are annually impacted by 1-2 major hurricanes, 3-4 large ship groundings, hundreds of small boat groundings, and tons of derelict fishing gear. After these acute disturbances, some fragments are subject to abrasion, scouring, and sedimentation which ultimately result in death. These damages can result in the loss of reef organisms, coral reef habitat, and ecosystem function, which can ultimately lead to reduced coastal protection, adverse economic impacts to local fisheries, and the elimination of tourism on which many coastal economies depend. However, if dislodged fragments can be collected and stabilized shortly after physical impact, the probability of survival increases substantially (Williams and Miller 2010). Stabilization (e.g., reattachment to hard substrate) has been demonstrated to significantly enhance the survival of small elkhorn or staghorn coral fragments. Elkhorn and staghorn corals and associated coral reef sessile benthic organisms can be reattached/secured in suitable habitat and/or managed for beneficial uses (e.g., research, nursery). This action calls for the expansion of existing programs and development of new regional emergency response and restoration networks with both domestic and international capability. These restoration networks should be regionally managed with local partners and have the resources available to respond immediately to reef impacts in order to stabilize corals, implement emergency restoration, and monitor long term effects. The ART considered a response to 50 percent of known physical disturbance events to be a reasonable number from both an ecological as well as a feasibility standpoint. Funding will be required to hire trained personnel, acquire appropriate vessels, and provide the needed materials for emergency response and restoration capability within each region (serving multiple jurisdictions as appropriate). Initiation: Immediately. Duration: On-going. Cost: U.S. Jurisdictions – $6 million (Start-up), $1.5 million (Annually); Internationally – $20 million (Start-up), $5 million (Annually).

b. ***Remove or stabilize rubble, debris, or other materials (e.g., derelict vessels or fishing gear):*** Marine debris accumulates over the years and presents a direct threat to corals. Often derelict vessels, lost traps, and other debris are found close to healthy stands of elkhorn and staghorn corals. This action would work collectively with the regional emergency response and restoration networks to use existing authorities to initiate an effort to remove known, existing debris that poses a direct threat to these two coral species and to develop a response, restoration, funding, and if necessary legal, capability to facilitate timely removal of newly identified/reported debris before it causes damage to coral reefs. Initiation: Immediately. Duration: On-going. Cost: Likely cost shared with action 19a.

ACTION 20: Reduce impacts from planned physical disturbances—No net loss from development projects

a. ***Develop coral transplant program:*** Elkhorn or staghorn corals attached to or in the vicinity of seawalls, marine debris, abandoned vessels, or reef areas subject to planned disturbance will be transplanted in accordance with guidelines developed for this purpose. In such cases all elkhorn and staghorn corals and associated reef organisms (corals, sponges) should be relocated by qualified personnel to an appropriate habitat outside of the impact area. These efforts will need to be coordinated with permitting agencies and consultants. Care should be taken to limit stress during

handling, and reattachments should strive to mimic natural reef conditions. Priority recipient areas will include ship grounding sites or other areas in need of restoration, as well as coral nurseries and areas selected for research. Initiation: Immediately. Duration: On-going. Cost: $100,000 annually.

b. ***Develop local guidelines for orphan Acropora spp.:*** This action will develop a set of guidelines for local resource agencies to use in dealing with orphan fragments of elkhorn and staghorn corals, ensuring that they are either stabilized on-site or transferred to a regional nursery. Initiation: 1 year. Duration: 1 year. Cost: $50,000.

ACTION 21: Implement Protective and Preventative Measures to Reduce Physical Impacts

a. ***Reduce impact of fishing gear/techniques:*** The direct impact of fishing gear on coral habitat varies among jurisdictions and fisheries. Nevertheless, trawls, nets, lines, fish traps, and lobster pots have potential for causing physical damage or entanglement. Fisheries regulations should be improved through new requirements, such as restricting fishing in areas near *Acropora* colonies, to eliminate impacts to coral reefs (Also addresses Objective 2: Criterion 8 –Regulatory Mechanisms). Additionally, active enforcement practices and MPAs should be established in areas of high quality elkhorn and staghorn coral reefs. Initiation: Immediately. Duration: On-going. Cost: Unknown.

b. ***Improve management of salvage operations to prevent impacts:*** In recent years, vessel salvage operations have been responsible for some of the major impacts to coral reefs. Statutes and regulations should be amended as appropriate to require marine salvors to obtain resource management agency authorization before removing any vessel grounded on sensitive benthic habitats (Also addresses Objective 2: Criterion 8 –Regulatory Mechanisms). Salvors should be required to implement specific actions, such as actively managing or using floating tow-lines to ensure no contact with the seafloor, directing prop wash in appropriate directions, and placing necessary anchors away from the reef, to minimize impacts to elkhorn and staghorn corals. This action would be operationalized by regional emergency response and restoration networks (Action 19a) Initiation: Immediately. Duration: On-going. Cost: Likely cost shared with Action 19a.

c. ***Improve nautical charts, ATONs, process of updating electronic charts:*** Appropriate amounts and types of aids to navigation (ATONs) should mark areas of known coral reefs likely to contain elkhorn or staghorn corals. Additionally, nautical and electronic charts should adequately indicate the location of coral reefs. Similar action must be taken within U.S. and foreign jurisdictions throughout the range of these species. Initiation: Immediately. Duration: On-going. Cost: Estimated $25,000 per region but dependent on scale.

d. ***Install/maintain mooring buoys:*** Mooring buoys have proven to be an effective means of reducing anchor impacts from recreational vessels. Additional funding and personnel are needed to place appropriate numbers and types of mooring buoys for all areas containing elkhorn or staghorn corals that are subject to anchor damage. Similar action must be taken within foreign jurisdictions throughout the ranges of these species. Initiation: Immediately. Duration: On-going. Cost: $2,500 per mooring buoy (initial installation), and $500 annually per mooring buoy (maintenance). Total cost of this action is dependent on scale. Some areas will need more/fewer buoys depending on use effort.

Interim Criterion 10: Predation

ACTION 22: Develop guidelines for snail (Coralliophila abbreviata) removal actions, and undertake snail removal actions in appropriate sites

Snail predation can be the primary mechanism of chronic tissue loss in elkhorn and staghorn coral colonies in some locations (or populations) (e.g., Williams and Miller 2006). Unlike most direct modes of tissue loss, such as disease or storm impacts, it can be averted by direct, local intervention. Removal of corallivorous snails, *Coralliophila abbreviata*, has been demonstrated to result in significant preservation of live elkhorn coral tissue (Miller 2001). Because the snails have limited mobility, significant effects in terms of tissue preservation are expected with reasonable levels of effort. Because these snails are abundant on alternative coral host species, it is not believed their removal from elkhorn and staghorn corals will significantly affect reef trophic structure. Formalized guidelines or "best practices" must be developed to ensure snail removal projects are conducted at appropriate sites (e.g., recovering populations, post-disturbance, during disease outbreaks, etc.) by appropriate expert personnel, and include appropriate data collection on the snails removed (e.g., numbers, sizes, sex ratio, and levels of effort) and evaluation (e.g., quantifying rates of re-colonization into removal area) in order to optimize removal efforts. Operational-scale snail removal projects should then proceed according to these guidelines. Initiation: Immediately. Duration: 1 year. Cost: $10,000.

ACTION 23: Evaluate risks and benefits of potential removal strategies for other corallivores

Other corallivores known to substantially impact elkhorn and staghorn corals include, but may not be limited to, threespot damselfish and the fireworm. Due to the greater mobility of these corallivores (and nocturnal habits for the worm), it is not clear if targeted removal efforts would be feasible for tissue preservation. First, protocols are needed to assess diversity, abundance, population dynamics, and impacts of other corallivores, and identify those of potential concern, which would be candidates for removal programs. Removal protocols should include methodologies for at least three types of populations: robust reference populations (e.g., thickets); degraded populations; and populations experiencing extensive recent tissue loss (e.g., due to disease outbreak, bleaching events, hurricanes, and/or other factors). Research is also needed to address potential impacts on (or feedbacks from) other reef biota including the third tropic level (predators of the corallivores) or alternate prey/host species. Last, rigorous pilot removal experiments should be undertaken in appropriate sites (i.e., with highly impacted elkhorn or staghorn coral populations) to determine if reasonable levels of effort can effect meaningful reductions in tissue loss. This increased knowledge should be synthesized into guidelines/recommendations for removal of other corallivores. Initiation: Immediately. Duration: 5 years. Cost: Unknown.

V. IMPLEMENTATION SCHEDULE

An implementation schedule is used to direct and monitor implementation and completion of recovery actions. Priorities in the first column of the following implementation schedule are assigned as follows:

Priority 1: An action that must be taken to prevent extinction or to prevent the species from declining irreversibly.

Priority 2: An action that must be taken to prevent a significant decline in population numbers or habitat quality, or to prevent other significant negative impacts short of extinction.

Priority 3: All other actions necessary to provide for full recovery of the species.

In general, the actions that directly address the abatement of major threats to the species or directly result in increasing the abundance of corals were given a priority ranking of one or two. Funding is estimated according to the number of years necessary to complete the task once implementation has begun and does not account for inflation. Estimates are based on information available at the time this plan was finalized; the amount needed to actually complete the task may change as specific actions are pursued. The provision of cost estimates is not meant to imply that appropriate levels of funding will necessarily be available for all elkhorn and staghorn recovery tasks. The costs associated with the various recovery tasks listed below are for those to be implemented in U.S. waters only. Costs associated with promotion of international action have not been estimated in all cases.

Disclaimer

The Implementation Schedule that follows outlines actions and estimated costs for the recovery program for elkhorn and staghorn corals, as set forth in the plan. It is a guide for meeting the recovery goals outlined in the plan. This schedule indicates action priorities, action numbers, action descriptions, duration of actions, the parties responsible for the actions (either funding or carrying out), and estimated costs. Parties with authority, responsibility, or expressed interest to implement a specific recovery action are identified in the Implementation Schedule. The listing of a party in the Implementation Schedule does not require the identified party to implement the action(s) or to secure funding for implementing the actions(s).

Table 3. Implementation Schedule of Recovery Actions for Threatened Elkhorn and Staghorn Corals.

IMPLEMENTATION SCHEDULE Threatened Elkhorn and Staghorn Corals										
Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
1	***Implement Outreach and Education***	2	FY1-5 and beyond	NMFS; EPA; NOAA; NPS; USGS; States/ Territories; Foreign nations; Local governments; NGOs	Dependent on scale	Dependent on scale	Dependent on scale	Dependent on scale	Dependent on scale	
2	***Coordinate Recovery Implementation***									
2a.	Recovery Coordinator	3	FY1-5 and beyond	NMFS	$150,000	$150,000	$150,000	$150,000	$150,000	
2b.	Central Elkhorn and Staghorn Coral Project/Data Repository	3	FY1-5 and beyond	NMFS	$25,000	N/A	N/A	N/A	N/A	6 months to develop; ongoing maintenance. Maintenance completed by Recovery Coordinator
3	***Conduct Strategic Research of Elkhorn and Staghorn Coral Biology***									
3a.	Genome Sequencing, Assembly and Annotation	3	FY1-5 and beyond	NOAA; Universities	$1,000,000 +	$1,000,000 +	$1,000,000 +	$1,000,000 +	$1,000,000 +	
3b.	Reproduction and Recruitment	2	FY1-5 and beyond	NOAA; Universities	$250,000	$250,000	$250,000	$250,000	$250,000	
3c.	Cellular Physiology and Biochemistry	3	FY1-5 and beyond	NOAA; Universities	$320,000	$320,000	$320,000	$320,000	$320,000	

IMPLEMENTATION SCHEDULE

Threatened Elkhorn and Staghorn Corals

Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
3d.	Symbiotic Relationships	3	FY1-5	NOAA; Universities	$250,000	$250,000	$250,000	$250,000	$250,000	
3e.	Immunity	3	FY1-5 and beyond	NOAA; Universities	$500,000	$500,000	$500,000	$500,000	$500,000	
4	***Develop Mapping and Inventory Products***									
4a.	Comprehensive Species Inventory Database	3	FY1-5 and beyond	NMFS	$25,000	$10,000	$10,000	$10,000	$10,000	6 months to develop; ongoing maintenance
4b.	Develop Remote Sensing Tools	3	FY1-5 and beyond	NOAA; USGS; NASA; Universities	Unknown	Unknown	Unknown	Unknown	Unknown	
5	***Monitor the Species and Their Environments***									
5a.	Develop a Range-Wide Monitoring Program	3	FY1-5 and beyond	NOAA; NPS; USGS; States/ Territories	$1,000,000	$1,000,000	$1,000,000	$1,000,000	$1,000,000	Scalable
5ai.	Habitat-Stratified Random Sampling for Abundance Assessment	3	FY1-5 and beyond	NOAA; NPS; USGS; Universities	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	
5aii.	Demographic Monitoring	3	FY1-5 and beyond	NOAA; NPS; USGS; Universities	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	
5aiii.	Evaluate Robust Reference Populations	3	FY1-5 and beyond	NOAA; NPS; USGS; Universities	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	
5aiv.	Periodically Monitor Water Quality Parameters Range-wide	3	FY1-5 and beyond	NOAA; NPS; USGS; Universities	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	Included in overall cost (see 5a)	

IMPLEMENTATION SCHEDULE

Threatened Elkhorn and Staghorn Corals

Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
5b.	Identify and Map Genotypes	3	FY1-5 and beyond	NOAA; Universities						
6	***Conduct Active Population Enhancement***									
6a.	Develop and Implement Comprehensive Restocking Plan									
6ai.	Scale up Field and Land-Based Nursery Culture Efforts	1	FY1-5 and beyond	NMFS; NOAA; NPS; NGOs; States/Territories; Universities; Zoos and Aquaria; Foreign nations	$10 million	$10 million	$10 million	$10 million	$10 million	Scalable
6aii.	Develop and Implement Guidelines/ Policies for Risk Management of Population Restocking	2	FY1-3	NMFS (development); NOAA; NPS; NGOs; States/Territories; Universities; Zoos and Aquaria; Foreign nations	$500,000	$500,000	$500,000	N/A	N/A	
6b.	Stabilize/ Reattach Both Storm and Anthropogenic-Generated Fragments	2	FY1-5 and beyond	NOAA; NPS; USCG; States/Territories	$2,000,000	$2,000,000	$2,000,000	$2,000,000	$2,000,000	Scalable
6c.	Enhance Genotypic Diversity in Known Genotypically Depauperate Populations	1	FY1-5 and beyond	NMFS; NOAA; NGOs; States/Territories; Universities; Zoos and Aquaria; Foreign nations	$150,000	$500,000	$500,000	$500,000	$500,000	Scalable

IMPLEMENTATION SCHEDULE

Threatened Elkhorn and Staghorn Corals

Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
6d.	Develop *Ex Situ* Conservation of Corals and Related Organisms	2	FY1-5 and beyond	NMFS; NOAA; NGOs; States/Terri-tories; Universities; Zoos and Aquaria; Foreign nations	Unknown	Unknown	Unknown	Unknown	Unknown	
6e.	Enhance Survival of Recruits	2	FY1-5 and beyond	NMFS; NOAA; NGOs; States/Terri-tories; Universities; Zoos and Aquaria; Foreign nations	Unknown	Unknown	Unknown	Unknown	Unknown	
6f.	Conduct Applied Population Enhancement Research									
6fi.	Land-Based Rearing of Corals	2	FY1-5 and beyond	NOAA; NGOs; Universities; Zoos and Aquaria	$500,000	$500,000	$500,000	$500,000	$500,000	Cost is per facility
6fii.	Larval Settlement, Recruitment, Grow-Out, and Restocking	1	FY1-5 and beyond	NOAA; NGOs; Universities; Zoos and Aquaria	$300,000	$300,000	$300,000	$300,000	$300,000	Cost is per facility

IMPLEMENTATION SCHEDULE

Threatened Elkhorn and Staghorn Corals

Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
7	***Understand Diseases Affecting Elkhorn and Staghorn Corals***	**1**	FY1-5 and beyond	NOAA; Universities; NGOs; States/Territories; Foreign nations	$500,000-$2,000,000	$500,000-$2,000,000	$500,000-$2,000,000	$500,000-$2,000,000	$500,000-$2,000,000	Cost is per watershed but is highly variable depending on management actions or need for greater certainty
8	***Respond to, Control, and Minimize Effects of Disease Events***									
8a.	Identify and Protect Apparently Resistant and Resilient Areas	1	FY1-5	NOAA; NPS; States/Territories; Foreign nations	$500,000	$500,000	$500,000	$500,000	$500,000	
8b.	Develop Capacity to Respond to Disease Events	1	FY1-5 and beyond	NOAA; NPS; States/Territories; Foreign nations	$750,000	$750,000	$750,000	$750,000	$750,000	Includes development of disease diagnostic tools
8c.	Develop and Test Effective Mitigation Approaches	1	FY1-5	NOAA; NPS; States/Territories; Foreign nations	$500,000	$500,000	$500,000	$500,000	$500,000	
8d.	Take Mitigative Action	1	FY1-5 and beyond	NOAA; NPS; States/Territories; Foreign nations	Unknown	Unknown	Unknown	Unknown	Unknown	

IMPLEMENTATION SCHEDULE

Threatened Elkhorn and Staghorn Corals

Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
9	***Develop and Implement U.S. and International Measures to Reduce Atmospheric CO_2 Concentrations***	1	FY1-5 and beyond	NOAA; EPA; Foreign nations	Unknown	Unknown	Unknown	Unknown	Unknown	Although crucial to future existence of corals, this action must take place at a scale broader than this recovery plan.
10	***Develop and implement Environmentally Sound Mechanisms to Reduce Local Impacts of Temperature Stress***	2	FY1-5 and beyond	NOAA; EPA; NPS; States/Territories; Foreign nations	Unknown	Unknown	Unknown	Unknown	Unknown	
11	***Research and Develop Mechanisms to Enhance Adaptation/Acclimation of Elkhorn and Staghorn Corals to Increases in Climate Stress***	2	FY1-5	NOAA; EPA; NPS; States/Territories; Foreign nations	Unknown	Unknown	Unknown	Unknown	Unknown	
12	***Restore, Protect, and Enhance Ecosystem Integrity and Function***									

IMPLEMENTATION SCHEDULE

Threatened Elkhorn and Staghorn Corals

Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
12a.	Enforce and Improve Existing Fishing Regulations	2	FY1-5 and beyond	NMFS; USCG; States/Terri-tories; Foreign nations	Unknown	Unknown	Unknown	Unknown	Unknown	
12b	Implement *Diadema antillarum* Restocking	2	FY 1-5	NOAA, NGOs, Universities, Zoos and Aquaria	$1,000,000	$1,000,000	$1,000,000	$1,000,000	$1,000,000	
12c.	Implement Effective MPAs	2	FY1-5 and beyond	NOAA; NPS; States/Terri-tories; Foreign nations	Unknown	Unknown	Unknown	Unknown	Unknown	
12d.	Conduct Research on Other Invertebrates	3	FY1-5	NOAA; NGOs; Universities	$100,000	$100,000	$100,000	$100,000	$100,000	
12e.	Conduct Research on *Palythoa caribaeorum*	3	FY1-5	NOAA; NGOs; Universities	$100,000	$100,000	$100,000	$100,000	$100,000	
13	***Address Sewage Discharge***									
13a	Identify, Determine, and Implement Appropriate Mechanism for Sewage Disposal in the U.S. and Caribbean	2	FY1-5	EPA; States/Terri-tories; Foreign nations	$10-20,000,000 (depending on the size of the facility and the extent of upgrades)	$10-20,000,000 (depending on the size of the facility and the extent of upgrades)	$10-20,000,000 (depending on the size of the facility and the extent of upgrades)	$10-20,000,000 (depending on the size of the facility and the extent of upgrades)	$10-20,000,000 (depending on the size of the facility and the extent of upgrades)	

IMPLEMENTATION SCHEDULE

Threatened Elkhorn and Staghorn Corals

Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
13b	Implement Tertiary Treatment of Wastewater in U.S. Jurisdiction	2	FY1-3	EPA; States/Terri-tories; Foreign nations	Varies	Varies	Varies	Varies	Varies	e.g., $14.8 million (for a new 160,000 gallons per day (gpd) sequential batch reactor treatment plant for 1000 equivalent dwelling units (homes), including plant and collection system)
14	***Develop and Implement Effective Watershed/ Land Use Management Plans for the Protection of Coral Reefs***	2	FY1-5 and beyond	NOAA; EPA; States/Terri-tories; Foreign nations	Dependent on scale	Dependent on scale	Dependent on scale	Dependent on scale	Dependent on scale	
15	***Restore and Maintain Mangrove and Seagrass Ecosystem Resources to Buffer Land-Based Influences***	2	FY1-5 and beyond	NOAA; EPA; States/Terri-tories; Foreign nations	Dependent on scale	Dependent on scale	Dependent on scale	Dependent on scale	Dependent on scale	

IMPLEMENTATION SCHEDULE

Threatened Elkhorn and Staghorn Corals

Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
16	***Study Organismal Response to Nutrients and Contaminants and Implement Appropriate Remedies***									
16a	Conduct Controlled Exposure Experiments	3	FY1-5 and beyond	NOAA; EPA; Universities; NGOs	$300,000-$500,000 per chemical (based on industry pricing for EPA protocols)	$300,000-$500,000 per chemical (based on industry pricing for EPA protocols)	$300,000-$500,000 per chemical (based on industry pricing for EPA protocols)	$300,000-$500,000 per chemical (based on industry pricing for EPA protocols)	$300,000-$500,000 per chemical (based on industry pricing for EPA protocols)	
16b	Develop Biocriteria	3	FY1-5	NOAA; EPA; Universities; NGOs	Cost shared with 16a	Cost shared with 16a	Cost shared with 16a	Cost shared with 16a	Cost shared with 16a	
17	***Develop and Implement a Pilot Regional Intergovernance Plan***									
17a	Develop a Pilot Regional Intergovernance Program in the U.S. Caribbean	3	FY 1-5 and beyond	NOAA; National Ocean Council; NPS; States/Territories; Foreign nations	Unknown	Unknown	Unknown	Unknown	Unknown	
17b	Develop a Strategic Marine Spatial Planning and Zoning Plan	3	FY 1-5 and beyond	NOAA; National Ocean Council; NPS; States/Territories	Unknown	Unknown	Unknown	Unknown	Unknown	

IMPLEMENTATION SCHEDULE

Threatened Elkhorn and Staghorn Corals

Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
18	***Enforce Existing or Develop New Regulations***									
18a	Enhance and Maximize Enforcement of Existing Regulations	2	FY1-5 and beyond	NOAA; USCG; NPS; EPA; COE; States/Territories; Foreign nations	$100,000 per officer	$100,000 per officer	$100,000 per officer	$100,000 per officer	$100,000 per officer	Costs are dependent on scale. Some areas will need more/fewer officers depending on enforcement needs.
18b	Adopt New Regulations	1	FY1-5 and beyond	NOAA; EPA; NPS; States/Territories; Foreign nations	Unknown	Unknown	Unknown	Unknown	Unknown	
19	***Respond to 50 Percent of Known Physical Disturbance Events***									
19a.	Develop and Implement Emergency Response and Restoration Networks	2	FY1-5 and beyond	NOAA; NPS; USCG; USGS; States/Territories; Foreign nations	$6,000,000 (U.S. Juris-dictions); $20 million (International)	$1,500,000 (U.S. juris-dictions); $5,000,000 (International)	$1,500,000 (U.S. juris-dictions); $5,000,000 (International)	$1,500,000 (U.S. juris-dictions); $5,000,000 (International)	$1,500,000 (U.S. juris-dictions); $5,000,000 (International)	
19b.	Remove or Stabilize Rubble, Debris, or Other Materials	2	FY1-5 and beyond	NOAA; NPS; USCG; USGS; States/Territories; Foreign nations	Likely cost-shared with 19a.	Likely cost-shared with 19a.	Likely cost-shared with 19a.	Likely cost-shared with 19a.	Likely cost-shared with 19a.	

IMPLEMENTATION SCHEDULE

Threatened Elkhorn and Staghorn Corals

Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
20	***Reduce Impacts from Planned Physical Disturbances– No Net Loss from Development Projects***									
20a.	Develop Coral Transplant Program	3	FY1-5 and beyond	NMFS; COE; States/Territories; Foreign nations	$100,000	$100,000	$100,000	$100,000	$100,000	
20b.	Develop Local Guidelines for Orphan *Acropora* spp.	3	FY1	NMFS; States/Territories; Foreign nations	$50,000	N/A	N/A	N/A	N/A	
21	***Implement Protective and Preventative Measures to Reduce Physical Impacts***									
21a.	Reduce Impact of Fishing Gear/Techniques	3	FY1-5 and beyond	NMFS; States/Territories; Foreign nations	Unknown	Unknown	Unknown	Unknown	Unknown	
21b.	Improve Management of Salvage Operations to Prevent Impacts	3	FY1-5 and beyond	NOAA; USCG; States/Territories	Likely cost shared with 19a	Likely cost shared with 19a	Likely cost shared with 19a	Likely cost shared with 19a	Likely cost shared with 19a	
21c.	Improve Nautical Charts, ATONs, Process of Updating Electronic Charts	3	FY1-5 and beyond	NOAA; USCG; States/Territories	$25,000	$25,000	$25,000	$25,000	$25,000	Costs are dependent on scale.

IMPLEMENTATION SCHEDULE

Threatened Elkhorn and Staghorn Corals

Recovery Action Number	Action Description	Priority Number	Action Duration	Responsible Parties	Estimated Fiscal Year Costs					Comments
					FY1	FY2	FY3	FY4	FY5	
21d.	Install and Maintain Mooring Buoys	3	FY1-5 and beyond	NOAA; USCG; NPS; States/Territories; Foreign nations	$3,000 per mooring buoy	$3,000 per mooring buoy	$3,000 per mooring buoy	$3,000 per mooring buoy	$3,000 per mooring buoy	Costs are dependent on scale. Some areas will need more/fewer buoys depending on use effort.
22	***Develop Guidelines for Snail (Coralliophila abbreviata) Removal Actions and Undertake Snail Removal Actions in Appropriate Sites***	2	FY1	NMFS	$10,000	N/A	N/A	N/A	N/A	
23	***Evaluate Risks and Benefits of Potential Removal Strategies for Other Corallivores***	3	FY1-5	NMFS	Unknown	Unknown	Unknown	Unknown	Unknown	

VI. LITERATURE CITED

Acker KL and M Risk. 1985. Substrate destruction and sediment production by the boring sponge *Cliona caribbaea* on Grand Cayman Island. Journal of Sedimentary Petrology 55:705-711.

Acropora Biological Review Team (BRT). 2005. Atlantic *Acropora* Status Review Document. Report to National Marine Fisheries Service, Southeast Regional Office. March 3, 2005. 152pp + App.

Adey WH. 1978. Coral reef morphogenesis: A multidimensional model. Science 202(4370): 831.

Aeby GS and Santavy DL. 2006. Factors affecting susceptibility of the coral *Montastraea faveolata* to black-band disease. Marine Ecology Progress Series 318: 103-110.

Albright R, Mason B, Langdon C. 2008. Effect of aragonite saturation state on settlement and post-settlement growth of *Porites astreoides* larvae. Coral Reefs 27: 485-490.

Albright R, Mason B, Miller M, Langdon C. 2010. Ocean acidification compromises recruitment success of the threatened Caribbean coral *Acropora palmata*. Proceedings of the National Academy of Sciences 107: 20400-20404.

Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proceedings of the Royal Society of London B. 276(1669): 3019-3025.

Anderson DL, Tyl MB, Otis RJ, Mayer TG, Sherman KM. 1998. Onsite wastewater nutrient reduction systems (OWNRS) for nutrient sensitive environments. In: Proceedings of the 8th National Symposium on Individual and Small Community Sewage Systems, March 8-10, 1009, Orlando, FL, pp. 436-445.

Anthony KRN, Hoogenboom MO, Maynard JA, Grottoli AG, Middlebrook R. 2009. Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. Functional Ecology 23(3): 539-550.

Arnold SN, Steneck RS, Mumby PJ. 2010. Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. Marine Ecology Progress Series 414: 91-105.

Arnold SN and Steneck RS. 2011. Settling into an increasingly hostile world: the rapidly closing ‘‘recruitment window’’ for corals. PloS ONE 6(12): e28681. doi: 10.1371/journal.pone.0028681

Aronson RB and Precht WF. 1997. Stasis, biological disturbance, and community structure of a Holocene coral reef. Paleobiology 23(3): 326-346.

Aronson RB and Precht WF. 2001. White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460(1): 25-38.

Aronson RB and Precht WF. 2006. Conservation, precaution, and Caribbean reefs. Coral Reefs 25: 441-450.

Auster PJ and Langton RW. 1999. The effects of fishing on fish habitat. In: L. Benaka (ed.).Fish Habitat: Essential Fish Habitat and Rehabilitation. American Fisheries Society, Bethesda, Maryland. p. 150-187.

Ayres Associates. 2000. Onsite wastewater nutrient reductions systems demonstration project. Phase II Addendum. Ayres Associates, Tampa, FL 28 pp.

Babcock R and Davies P. 1991. Effects of sedimentation on settlement of *Acropora millepora*. Coral Reefs 9: 205-208.

Bak RPM and Eys G. 1975. Predation of the sea urchin *Diadema antillarum* Philippi on living coral. Oecologia 20(2): 111-115.

Bak RPM and Criens S. 1982. Survival after fragmentation of colonies of *Madracis mirabilis*, *Acropora palmata* and *A. cervicornis* (Scleractinia) and the subsequent impact of a coral disease. Proceeding of the 4th International Coral Reef Symposium 2: 221-227.

Bak RPM, Nieuwland G, Meesters EH. 2009. Coral growth rates revisited after 31 years: What is causing lower extension rates in *Acropora palmata*? Bulletin of Marine Science 84(3): 287-294.

Baums IB. 2008. A restoration genetics guide for coral reef conservation. Molecular Ecology 17(12): 2796-2811.

Baums IB, Miller MW, Szmant AM. 2003a. Ecology of a corallivorous gastropod, *Coralliophila abbreviata*, on two scleractinian hosts. I: Population structure of snails and corals. Marine Biology 142(6): 1083-1091.

Baums IB, Miller MW, Szmant AM. 2003b. Ecology of a corallivorous gastropod, *Coralliophila abbreviata*, on two scleractinian hosts. II. Feeding, respiration and growth. Marine Biology 142(6): 1093-1101.

Baums IB, Hughes CR, Hellberg ME. 2005a. Mendelian microsatellite loci for the Caribbean coral *Acropora palmata*. Marine Ecology Progress Series 288: 115-127.

Baums IB, Miller MW, Hellberg ME. 2005b. Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. Molecular Ecology 14: 1377-1390.

Baums IB, Miller MW, Hellberg ME. 2006. Geographic variation in clonal structure of a reef-building Caribbean coral, *Acropora palmata*. Ecological Monographs 76: 503-519

Baums IB, Durante M, Brown L, Pinzon JH. 2009. Nine novel, polymorphic microsatellite markers for the study of threatened Caribbean Acroporid corals. Molecular Ecology Resources 9(4): 1155-1158.

Baums IB, Johnson ME, Devlin-Durante MK, Miller MW. 2010. Host population genetic structure and zooxanthellae diversity of two reef-building coral species along the Florida Reef Tract and wider Caribbean. Coral Reefs 29: 835–842.

Becker LC and Mueller E. 2001. The culture, transplantation and storage of *Montastraea faveolata*, *Acropora cervicornis* and *Acropora palmata*: What we have learned so far. Bulletin of Marine Science 69(2): 881-896.

Bielmyer GK, Grosell M, Bhagooli R, Baker AC, Langdon C, Gillette P, Capo TR. 2010. Differential effects of copper on three species of scleractinian corals and their algal symbionts (*Symbiodinium* spp.). Aquatic Toxicology 97: 125-133.

Birrell CL, McCook LJ, Willis BL. 2005. Effects of algal turfs and sediment on coral settlement. Marine Pollution Bulletin 51(1-4): 408-414.

Birrell CL, McCook LJ, Willis BL, Diaz-Pulido GA. 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Oceanography and Marine Biology: an Annual Review 46: 25-63.

Blainville, H. M. de. 1830. Zoophytes. Dictionnaire des sciences naturelles. Paris, Volume 60.

Blanchon P, Eisenhauer A, Fietzke J, Liebetrau Z. 2009. Rapid sea-level rise and reef back-stepping at the close of the last interglacial highstand. Nature 458: 881-885.

Boehm PD, Douglas GS, Loreti CP. 1995. Managing the NRDA process: challenges in establishing causation and injury. Proceedings for the Toxic Substances in Water Environments: Assessment and Control. Water Environment Federation. Pp. 7-20.

Boehm PD, Galvani PB, O'Donnell PJ. 1995. Scientific and legal conundrums in establishing injury and damages: the natural resource damage assessment regulations. In: Stewart RB (Eds.) *Natural Resource Damages: A Legal, Economic, and Policy Analysis.* The National Legal Center for the Public Interest. Pp. 31-60.

Bourne GC. 1900. The Anthozoa. In E. R. Lankester (ed.), A Treatise on Zoology, Pt. II, The Porifera and Coelentera. Adam and Charles Black, London. p. 1-84.

Brawley SH and Adey WH. 1977. Territorial behavior of threespot damselfish *(Eupomacentrus planifrons)* increases reef algal biomass and productivity. Environmental Biology of Fishes 2(1): 45-51.

Brazeau DA, Sammarco PW, Gleason DF. 2005. A multi-locus genetic assignment technique to assess sources of *Agaricia agaricites* larvae on coral reefs. Marine Biology 47(5): 1141-1148.

Bright AJ, Williams DE, Kramer KL, Miller MW. 2013. Recovery of *Acropora palmata* in Curacao: a comparison with the Florida Keys. Bulletin of Marine Science 89(3):747-757.

Bruckner AW. 2000. New Threat to Coral Reefs: Trade in Coral Organisms. Issues in Science and Technology.

Bruckner AW (Ed.). 2002. Proceedings of the Caribbean *Acropora* Workshop: Potential Application of the U.S. Endangered Species Act as a Conservation Strategy. Silver Spring, MD: NOAA Technical Memorandum NMFS-OPR-24.

Bruckner AW and Bruckner RJ. 1997. Outbreak of coral disease in Puerto Rico. Coral Reefs 16(4): 260.

Bruckner RJ, Bruckner AW, Williams Jr EH. 1997. Life history strategies of *Coralliophila abbreviata* Lamarck (Gastropoda: Coralliophilidae) on the southeast coast of Puerto Rico. Proceedings of the 8th International Coral Reef Symposium. Pp. 627-632.

Bruckner AW, Hill R, Bruckner RJ. 2008. Fates of restored *Acropora palmata* fragments at the *M/V Fortuna Reefer* grounding site, Mona Island Puerto Rico: Lessons learned over 10 years. Abstract: 11th Int Coral Reef Symposium, Ft. Lauderdale.

Bruno JF, Petes LE, Drew Harvell C, Hettinger A. 2003. Nutrient enrichment can increase the severity of coral diseases. Ecology Letters 6(12): 1056-1061.

Bruno JF, Selig ER, Casey KS, Page CA, Willis BL, Harvell CD, Sweatman H, Melendy AM. 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. PLoS Biol 5(6): e124. doi:10.1371/ journal.pbio.0050124

Bythell JC, Bythell M, Gladfelter EH. 1993. Initial results of a long-term coral reef monitoring program: Impact of Hurricane Hugo at Buck Island Reef National Monument, St. Croix, U. S. Virgin Islands. Journal of Experimental Marine Biology and Ecology 172: 171-1832.

Cairns SD. 1982. Stony corals (Cnidaria: Hydrozoa, Scleractinia) of Carrie Bow Cay, Belize. In: Rutzler K and Macintyre IG (eds.) The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. Smithsonian Institution Press, Washington, D.C. pp. 271-302.

Caldeira K and Wickett ME. 2003. Anthropogenic carbon and ocean pH. Nature 425(6956): 365-365.

Camp E and Fraser D. 2012. Influence of conservation education dive briefings as a management tool on the timing and nature of recreational SCUBA diving impacts on coral reefs. Ocean and Coastal Management 61: 30-37.

Carilli JE, Norris RD, Black BA, Walsh SM, McField M. 2009. Local stressors reduce coral resilience to bleaching. PLoS ONE 4(7): e6324. doi:10.1371/journal.pone.0006324CDIAC. 2009. Data available at: http://cdiac.ornl.gov/oceans/doc.html

Carollo C, Reed DJ, Ogden JC, Palandro D. 2009. The importance of data discovery and management in advancing ecosystem-based management. Marine Policy 33: 651-653.

Carpenter KE et al. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321: 560-563.

Carpenter RC. 1990. Mass mortality of *Diadema antillarum* I. Long-term effect on sea urchin population-dynamics and coral reef algal communities. Marine Biology 104: 67-77.

Carpenter RC and Edmunds PJ. 2006. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. Ecology Letters 9(3): 271-280.

Cervino JM, Hayes RL, Polson SW, Polson SC, Goreau TJ, Martinez RJ, Smith GW. 2004. Relationship of *Vibrio* species infection and elevated temperatures to yellow blotch/band disease in Caribbean corals. Applied and Environmental Microbiology 70(11): 6855-6864.

Chalker BE. 1977. Daily variation in the calcification capacity of *Acropora cervicornis*. Proceedings of the 3rd International Coral Reef Symposium pp. 417-23.

Cohen AL, McCorkle DC, de Putron S. 2007. The impact of seawater saturation state on early skeletal development in larval corals: Insights into scleractinian biomineralization. Proceedings of the American Geophysical Union 2007 Fall Meeting. [np].

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. Geochemistry, Geophysics, Geosystems 10: Q07005. doi:10.1029/2009GC002411.

Coles SL and Seapy DG. 1998. Ultra-violet absorbing compounds and tumorous growths on acroporid corals from Bandar Khayran, Gulf of Oman, Indian Ocean. Coral Reefs 17(2): 195-198.

Collier C, Dodge R, Gilliam D, Gracie K, Gregg L, Jaap W, Mastry M, Poulos N. 2007. Rapid Response and Restoration for Coral Reef Injuries in Southeast Florida: Guidelines and Recommendations Southeast Florida Coral Reef Initiative. 57 pp.

Cormier SM. 2006. Ecoepidemiology: a means to safeguard ecosystem services that sustain human welfare. Ecotoxicology, Ecological Risk Assessment and Multiple Stressors. Pp. 57-72.

Cormier SM and Suter G. 2008. A framework for fully integrating environmental assessment. Environmental Management 42: 543-556.

Côté IM and Maljković A. 2010. Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. Marine Ecology Progress Series 404: 219-225.

Crowder LB, Osherenko G, Young OR, Airame S, Norse EA, Baron N, Day JC, Douvere F, Ehler CN, Halpern BS, Langdon SJ, McLeod KL, Ogden JC, Peach RE, Rosenberg AA, Wilson JA. 2006. Resolving mismatches in U.S. ocean governance. Science 313: 617-618.

Croquer A, Bastidas C, Lipscomp D, Rodriguez-Martinez RE, Jordan-Dahlgren E, Guzman H. 2006. First report of folliculinid ciliates affecting Caribbean scleractinian corals. Coral Reefs 25: 187-191.

Curran HA, Smith DP, Meigs LC, Pufal AE, Greer LM, Walton Smith FG. 1994. The health and short-term change of two coral patch reefs, Fernandez Bay, San Salvador Island, Bahamas. Global Aspects of Coral Reefs: Health, Hazard and History. University of Miami, Rosenstiel School of Marine and Atmospheric Science, Miami (USA). Pp. F1-F79.

Curry JA. 2008. Potential increase hurricane activity in a greenhouse warmed world. In: MacCracken MC, Moore F, Topping JC (Eds.), Sudden and Disruptive Climate Change. Earthscan Publications Ltd, New York.

Danovaro R, Bongiorni L, Corinaldesi C, Giovannelli D, Damiani E, Astolfi P, Greci L, Pusceddu A. 2008. Sunscreens cause coral bleaching by promoting viral infections. Environmental Health Perspectives 116: 441-447.

Davis GE. 1977. Anchor damage to a coral reef on the coast of Florida. Biological Conservation 11(1): 29-34.

Davis GE. 1982. A century of natural change in coral distribution at the Dry Tortugas: A comparison of reef maps from 1881 and 1976. Bulletin of Marine Science 32(2): 608-623.

Davis M, Gladfelter E, Lund H, Anderson M. 1985. Geographic range and research plan for monitoring white band disease. VIRMC Tech. Rep. # 6. U.S. National Park Service.

De'ath G, Lough JM, Fabricius KE. 2009. Declining coral calcification on the Great Barrier Reef. Science 323(5910): 116-119.

de Ruyter van Steveninck ED and Bak RPM. 1986. Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. Marine Ecology Progress Series 34: 87-94.

Donner SD. 2009. Coping with commitment: projected thermal stress on coral reefs under different future scenarios. PLoS ONE 4: e5712. doi: 10.1371/journal.pone.0005712.

Donner SD, Skirving WJ, Little CM, Oppenheimer M, Hoegh-Guldberg O. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. Global Change Biology 11(12): 2251-2265.

Donner SD, Knutson TR, Oppenheimer M. 2007. Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. Proceedings of the National Academy of Science 104: 5483–5488.

Donohue MJ, Boland RC, Sramek CM, Antonelis GA. 2001. Derelict fishing gear in the Northwestern Hawaiian Islands: Diving surveys and debris removal in 1999 confirm threat to coral reef ecosystems. Marine Pollution Bulletin 42(12): 1301-1312.

Douglas AE. 2003 Coral bleaching - how and why? Marine Pollution Bulletin 46: 385-392.

Downs CA. 2005. Cellular diagnostics and its application to aquatic and marine toxicology. In: Ostrander (Ed.), Techniques in Aquatic Toxicology Vol. II. CRC Press, Boca Raton. Pp 181-207.

Downs C, Fauth J, Halas J, Dustan P, Bemiss J, Woodley CM. 2002. Oxidative stress and seasonal coral bleaching. Free Radical Biology and Medicine 33: 533-543.

Downs CA, Downs AG, Jonas RB, Briggs K, Capo T, Woodley CM. 2005a. IMCOMP-P: an assay for coral immuno-competence. In: Ostrander (Ed.) Techniques in Aquatic Toxicology Vol. I. CRC Press, Boca Raton. Pp. 301-313.

Downs CA, Woodley CM, Richmond RH, Lanning LL, Owen, R. 2005b. Shifting the Paradigm for Coral Reef 'Health' Assessment. Marine Pollution Bulletin 51: 486-494.

Downs C, Kramarsky-Winter E, Martinez J, Kushmaro A, Woodley CM, Loya Y, Ostrander GK. 2009. Symbiophagy as a cellular mechanism for coral bleaching. Autophagy 5: 211-216.

Downs CA, Fauth JE, Downs VD, Ostrander GK. 2010. In vitro cell-toxicity screening as an alternative animal model for coral toxicology: effects of heat stress, sulfide, rotenone, cyanide, and cuprous oxide on cell viability and mitochondrial function. Ecotoxicology 19: 171-184.

Downs CA, Woodley CM, Fauth J, Knutson S, Burtcher M, May LA, Avadanei A, Higgins J, Ostrander G. 2011. A survey of environmental pollutants and cellular-stress markers of *Porites astreoides* at six sites in St. John U.S. Virgin Islands. Ecotoxicology 20: 1914-1931.

Dustan P. 1977. Vitality of reef coral populations off Key Largo, Florida: Recruitment and mortality. Environmental Geology 2(1): 51-58.

Dustan P. 1985. Community structure of reef-building corals in the Florida Keys: Carysfort Reef, Key Largo and Long Key Reef, Dry Tortugas. Atoll Research Bulletin 288: 1-27.

Dutra LXC, Kikuchi RKP, Leao Z. 2006. Effects of sediment accumulation on reef corals from Abrolhos, Bahia, Brazil. Journal of Coastal Research 2: 633-638.

Eakin CM, Lough JM, Heron SF. 2009. Climate, weather and coral bleaching. In: Lough JM and Van Oppen M (eds.) Coral bleaching: patterns, processes, causes and consequences. Springer Ecological Studies 205:41–67.

Eakin CM et al. 2010. Caribbean Corals in Crisis: Record Thermal Stress, Bleaching, and Mortality in 2005. PLoS ONE 5(11): e13969. doi: 10.1371/journal.pone.0013969.

Edmunds PJ and Carpenter RC. 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proceedings of the National Academy of Sciences 98(9): 5067-5071.

Edwards AJ and Gomez ED. 2007. Reef Restoration Concepts and Guidelines: making sensible management choices in the face of uncertainty. Coral Reef Targeted Research & Capacity Building for Management Programme: St Lucia, Australia. iv + 38 pp.

Edwards HJ, Elliott IA, Eakin CM, Irikawa A, Madin JS, McField M, Morgan JA, Van Woesik R, Mumby PJ. 2011. How much time can herbivore protection buy for coral reefs under realistic regimes of hurricanes and coral bleaching? Global Change Biology 17: 2033–2048.

Efrony R, Atad I, Rosenberg E. 2009. Phage Therapy of Coral White Plague Disease: Properties of Phage BA3. Current Microbiology 58: 139-145.

EIA (Energy Information Administration). 2005. Overview of U.S. Legislation and Regulations Affecting Offshore Natural Gas and Oil Activity. Energy Information Administration, Office of Oil and Gas, Herndon, Virginia. September 2005.

Epstein N, Bak RPM, Rinkevich B. 2001. Strategies for gardening denuded coral reef areas: The applicability of using different types of coral material for reef restoration. Restoration Ecology 9(4): 432-442.

Fabricius KE. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50(2): 125-146.

Fabricius KE, Wild C, Wolanski E, Abele D. 2003. Effects of transparent exopolymer particles and muddy terrigenous sediments on the survival of hard coral recruits. Estuarine Coastal and Shelf Science 57(4): 613-621.

Fabry VJ, Seibel BA, Feely RA, Orr JC. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. ICES Journal of Marine Science 65: 414-432.

Fairbanks RG. 1989. A 17,000-year glacio-eustatic sea level record - influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. Nature 342: 637-642.

Florida Fish & Wildlife Conservation Commission (FWC). 2008. Wildlife 2060: What's at Stake for Florida. Available at www.MyFWC.com/wildlife2060.

FWC. 2007. Genetic Policy for the Release of Finfishes in Florida. Florida Fish and Wildlife Research Institute Publication Number IHR-2007-001.

Foreman CM and Covert JS. 2003. Linkages between dissolved organic matter consumption and bacterial community structure. In: Findlay SEG and Sinsabaugh RL (eds.). Aquatic Ecosystems: Interactivity of Dissolved Organic Matter. Academic Press, San Diego, CA. pp. 343-359.

Fukami H, Budd AF, Levitan DR, Jara J, Kersanach R, Knowlton N. 2004. Geographic differences in species boundaries among members of the *Montastraea annularis* complex based on molecular and morphological markers. Evolution 58(2): 324-337.

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term region-wide declines in Caribbean corals. Science 301: 958-960.

Garcia RPU, Alvarado EMC, Acosta MA. 1996. Growth of the coral *Acropora palmata* (Lamarck, 1886) in the Corales del Rosario National Natural Park, Colombian Caribbean. Boletin de Investigaciones Marinas y Costeras 25: 7-18.

Gates R, Baghdasarian G, Muscatine L. 1992. Temperature stress causes host cell detachment in symbiotic cnidarians: implications for coral bleaching. Biological Bulletin 182: 324-332.

Geiser DM, Taylor JW, Ritchie KB, Smith GW. 1998. Cause of sea fan death in the West Indies. Nature 394:137-138.

Geister J. 1992. Modern reef development and Cenozoic evolution of an oceanic island/reef complex: Isla de Providencia (Western Caribbean sea, Colombia). Facies 27(1): 1-69.

Gil-Agudelo DL, Smith GW, Weil E. 2006. The white band disease type II pathogen in Puerto Rico. Revista de Biologia Tropical 54: 59-67.

Gilmore MD and Hall BR. 1976. Life history, growth habits, and constructional roles of *Acropora cervicornis* in the patch reef environment. Journal of Sediment Petrology 46: 519-522.

Gladfelter EH 1983. Skeletal development in *Acropora cervicornis* II: Diel patterns of calcium carbonate accretion. Coral Reefs 2: 91-100.

Gladfelter EH. 2007. Skeletal development in *Acropora palmata* (Lamarck 1816): a scanning electron microscope (SEM) comparison demonstrating similar mechanisms of skeletal extension in axial versus encrusting growth. Coral Reefs 26(4): 883-892.

Gladfelter EH, Monahan RK, Gladfelter WB. 1978. Growth rates of five reef-building corals in the northeastern Caribbean. Bulletin of Marine Science 28(4): 728-734.

Gladfelter WB. 1982. White-Band Disease in *Acropora palmata*: Implications for the structure and growth of shallow reefs. Bulletin of Marine Science 32(2): 639-643.

Gledhill DK, Wanninkhof R, Millero FJ, Eakin M. 2008. Ocean acidification of the Greater Caribbean Region 1996–2006. Journal of Geophysical Research 113: C10031. doi:10.1029/2007JC004629.

Glynn PW. 1990. Feeding ecology of selected coral-reef macroconsumers: patterns and effects on coral community structure. In: Z. Dubinsky (Ed.). Ecosystems of the World, Coral Reefs. Elsevier, New York. Pp. 439-452.

Glynn PW, Almodovar LR, Gonzalez JG. 1964. Effects of Hurricane Edith on marine life in La Parguera, Puerto Rico. Caribbean Journal of Science 4(2&3): 335-345.

Goldberg WM. 1973. The ecology of the coral-octocoral communities off the southeast Florida coast: geomorphology, species composition, and zonation. Bulletin of Marine Science 23(3): 465-488.

Goreau TF. 1959. The ecology of Jamaican coral reefs: I. species composition and zonation. Ecology 40(1): 67-90.

Goreau NI, Goreau TJ, Hayes RL. 1981. Settling, survivorship and spatial aggregation in planulae and juveniles of the coral *Porites porites* (Pallas). Bulletin of Marine Science 31: 424-435.

Green SJ, Akins JL, Côté IM. 2011. Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. Marine Ecology Progress Series 433: 159-167.

Greer L, Jackson JE, Curran HA, Guilderson T, Teneva L. 2009. How vulnerable is *Acropora cervicornis* to environmental change? Lessons from the early to middle Holocene. Geology 37(3): 263-266.

Griffin DW, Kellogg CA, Garrison VH, Shinn EA. 2002. The global transport of dust – An intercontinental river of dust, microorganisms and toxic chemicals flows through the Earth's atmosphere. American Scientist 90(5): 398-398.

Griffin DW, Kellogg CA, Garrison VH, Lisle JT, Borden TC, Shinn EA. 2003. Atmospheric microbiology in the northern Caribbean during African dust events. Aerobiologia 19:143-157.

Grober-Dunsmore R, Bonito V, Frazer TK. 2006. Potential inhibitors to recovery of *Acropora palmata* populations in St. John, US Virgin Islands. Marine Ecology Progress Series 321: 123-132.

Grober-Dunsmore R, Bonito V, Frazer TK. 2007. Discernment of sexual recruits is not critical for assessing population recovery of *Acropora palmata*. Marine Ecology Progress Series 335: 233-236.

Grottoli AG, Rogdriguez LJ, Palardy JE. 2006. Heterotrophic plasticity and resilience in bleached corals. Nature 440: 1186-1189.

Guinotte JM, Buddemeier RW, Kleypas JA. 2003. Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific Basin. Coral Reefs 22(4): 551-558.

Hagedorn M, Carter VL, Steyn RA, Krupp D, Leong J, Lang RP, Tiersch TR. 2006a. Preliminary studies of sperm cryopreservation in the mushroom coral, *Fungia scutaria*. Cryobiology 52:454-8.

Hagedorn M, Pan R, Cox E, Hollingsworth L, Lewis TD, Leong JC, Krupp DA, Mazur P, Rall WF, MacFarlane D, Fahy G, Kleinhans FW. 2006b. Coral larvae conservation: Physiology and reproduction. Cryobiology 52:33-47.

Hahn ME and Stegeman JE. 1999. Molecular biology and biotechnology in marine toxicology. Opportunities for Environmental Applications of Marine Biology. Proceedings of the October 5-6, 1999, Workshop. WHOI-R-99-00: 112-125.

Halas JC. 1985. An unique mooring system for reef management in the Key Largo National Marine Sanctuary. Proceedings of the Fifth International Coral Reef Congress, Tahiti 27 May - 1 June 1985 4: 237-242.

Halas JC. 1997. Advances in environmental mooring technology. Proceedings of the 7th International Coral Reef Symposium II. pp. 1995-2000.

Halley RB, Reich CT, Hickey TD. 2001. Coral reefs in Honduras: Status after Hurricane Mitch. USGS Open File Report 01-133. 4 pp.

Harrington L, Fabricius K, De'ath G, and Negri A. 2004. Recognition and selection of settlement substrata determine post-settlement survival in corals. Ecology 85(12): 3428-3437.

Harvell CD, Kim K, Burkholder JM, Colwell RR, Epstein PR, Grimes DJ, Hofmann EE, Lipp EK, Osterhaus A, Overstreet RM, Porter JW, Smith GW, Vasta GR. 1999. Emerging marine diseases – Climate links and anthropogenic factors. Science 285(5433): 1505-1510.

Havenhand JN, Buttler FR, Thorndyke MC, Williamson JE. 2008. Near-future levels of ocean acidification reduce fertilization success in a sea urchin. Current Biology 18(15): R651-R652.

Hayes JA. 1990. Distribution, movement and impact of the corallivorous gastropod *Coralliophila abbreviata* (Lamarck) on a Panamanian patch reef. Journal of Experimental Marine Biology and Ecology 142(1-2): 25-422.

Hedges, JI. 2002. Why dissolved organics matter. In: Hansell DA and Carlson CA (Eds.) Biogeochemistry of Marine Dissolved Organic Matter. Academic Press, San Diego, CA. Pp. 1-33.

Highsmith RC. 1982. Reproduction by fragmentation in corals. Marine Ecology Progress Series 7(29): 207-226.

Highsmith RC, Riggs AC, D'Antonio CM. 1980. Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. Oecologia 46: 322-329.

Hodel E and Vargas-Ángel B. 2007. Histopathological Assessment and Comparison of Sedimentation and Phosphate Stress in the Caribbean Staghorn Coral, *Acropora cervicornis*. Microscopy and Microanalysis 13(S02): 220-221.

Hoegh-Guldberg O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50: 839-866.

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318(5857): 1737-1742.

Hubbard JAEB and Pocock YP. 1972. Sediment rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. International Journal of Earth Sciences 61(2): 598-626.

Hudson JH. 2000. First aid for massive corals infected with black band disease, *Phormidium corallyticum*: An underwater aspirator and post-treatment sealant to curtail reinfection. In: Hallock and French (Eds). Diving for Science. Proceedings of the 20th Annual Scientific Diving Symposium, American Academy of Underwater Sciences. St Pete Beach, Florida.

Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265(5178): 1547-1551.

Intergovernmental Panel on Climate Change (IPCC). 2007. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland. Pp. 104.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the IPCC 5th Assessment Report. http://www.ipcc.ch/report/ar5/wg1/

Itzkowitz M. 1978. Group organization of a territorial damselfish, *Eupomacentrus planifrons*. Behaviour 65(1/2): 125-137.

Jaap WC. 1974. Scleractinian growth rate studies. 17th Proceedings of the Fl Keys Coral Reef Workshop. Florida Department of Natural Resources Coastal Coordinating Council.

Jaap WC. 1984. The Ecology of South Florida Coral Reefs: A Community Profile. US Fish and Wildlife Service. FWS/OBS-82/08.

Jaap WC and Wheaton J. 1975. Observations on Florida reef corals treated with fish-collecting chemicals. Florida Marine Research Publication 10:1–17.

Jaap WC, Lyons WG, Dustan P, Halas JC. 1989. Stony coral (Scleractinia and Milleporina) community structure at Bird Key Reef, Ft. Jefferson National Monument, Dry Tortugas, Florida. Florida Marine Research Publication 46.

Jackson JBC. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. American Naturalist 111: 743-767.

Jackson JBC. 1986. Modes of dispersal of clonal benthic invertebrates: Consequences for species' distributions and genetic structure of local populations. Bulletin Marine Science 39: 588-606.

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR. 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. Science 293(5530): 629-638.

Jackson JBC. 2008. Ecological extinction and evolution in the brave new ocean. Proceedings of the National Academy of Sciences of the United States of America 105: 11458-11465.

Jackson JBC, Donovan MK, Cramer KL, Lam VV (editors). 2014. Status and Trends of Caribbean Coral Reefs: 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.

Jayewardene D, Donahue MJ, Birkeland C. 2009. Effects of frequent fish predation on corals in Hawai'i. Coral Reefs 28: 499-506.

Jennings S and Lock JM. 1996. Population and ecosystem effects of reef fishing. In: Polunin NVC and Roberts CM (Eds.). Reef Fisheries. Chapman and Hall, New York. Pp. 193-218.

Jennings S and Polunin NVC. 1996. Impacts of fishing on tropical reef ecosystems. Ambio 25(1): 44-49.

Johns GM, Leeworthy VR, Bell FW, and Bonn MA. 2003. Socioeconomic Study of Reefs in Southeast Florida, Final Report, October 19, 2001, as revised April 18, 2003.

Johnston L and Miller MW. 2007. Variation in life-history traits of the corallivorous gastropod *Coralliophila abbreviata* on three coral hosts. Marine Biology 150: 1215-1225.

Jokiel PL, Rodgers KS, Kuffner IB, Andersson AJ, Cox EF, Mackenzie FT. 2008. Ocean acidification and calcifying reef organisms: a mesocosm investigation. Coral Reefs 27(38): 473-483.

Jones GP and Syms C. 1998. Disturbance, habitat structure, and ecology of fishes on coral reefs. Australian Journal of Ecology 3: 287-297.

Jones RJ and Kerswell AP. 2003. Phytotoxicity of Photosystem II (PSII) herbicides to coral. Marine Ecology-Progress Series 261: 149-159.

Jordan-Dahlgren E and Rodriguez-Martinez RE. 1998. Post-hurricane initial recovery of *Acropora palmata* in two reefs of the Yucatan Peninsula, Mexico. Bulletin of Marine Science 63(1): 213-228.

Joyce AR and Palsson BO. 2006. The model organism as a system: integrating "omics" data sets. Nature Reviews 7: 198-210.

Kaufman. 1977. The three spot damselfish: effects on benthic biota of Caribbean coral reefs. In: Proceedings of the 3rd International Coral Reef Symposium 1: 559-564.

Kellogg CA, Griffin DW, Garrison VH, Peak KK, Royall N, Smith RR, and Shinn EA. 2004. Characterization of aerosolized bacteria and fungi from desert dust events in Mali, West Africa. Aerobiologia 20:99-110.

Kendall JJ, Powell EN, Connor SJ, Bright TJ. 1983. The effects of drilling fluids (muds) and turbidity on the growth and metabolic state of the coral *Acropora cervicornis*, with comments on methods of normalization for coral data. Bulletin of Marine Science 33(2): 336-352.

Kennish MJ. 1997. Practical Handbook of Estuarine and Marine Pollution (Marine Science Series). CRC Press, Boca Raton, FL.

Kiessling W and Baron-Szabo RC. 2004. Extinction and recovery patterns of scleractinian corals at the Cretaceous-Tertiary boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 214(3): 195-223.

Kleypas JA and Eakin CM. 2007. Scientists' perceptions of threats to coral reefs: results of a survey of coral reef researchers. Bulletin of Marine Science 80 (2): 419-436.

Kleypas JA, McManus JW, Meñez LA. 1999. Environmental limits to coral reef development: Where do we draw the line? American Zoologist 39: 146-159.

Kline DI, Kuntz NM, Breitbart M, Knowlton N, and Rohwer F. 2006. Role of elevated organic carbon levels and microbial activity in coral mortality. Marine Ecology Progress Series 314: 119-125.

Kline DI and Vollmer SV. 2011. White Band Disease (type I) of endangered Caribbean acroporid corals is caused by pathogenic bacteria. Scientific Reports 1: 7. doi: 10.1038/srep00007.

Klumpp DW, Pulfrich A. 1989. Trophic significance of herbivorous macroinvertebrates on the central Great Barrier Reef. Coral Reefs 8:135-144.

Knowlton N. 1992. Thresholds and multiple stable states in coral reef community dynamics. American Zoologist 32: 674-682.

Knowlton N, Lang JC, Keller BD. 1990. Case study of natural population collapse: post-hurricane predation on Jamaican staghorn corals. Smithsonian Contributions to Marine Science 31: 25.

Knowlton N, Lang JC, Rooney CM, Clifford P. 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. Nature 294: 251-252.

Knowlton N, Weil E, Weigt LA, Guzman HM. 1992. Sibling species in *Montastraea annularis*, coral bleaching, and the coral climate record. Science 255: 330-333.

Knutson TR, Sirutis JJ, Garner ST, Vecchi GA, Held IM. 2008. Simulated reduction in Atlantic hurricane frequency under twenty-first-century warming conditions. Nature Geoscience 1: 359-364.

Knutson S, Downs CA, Richmond RH. 2012. Concentrations of Irgarol in selected marinas of Oahu, Hawaii and effects on settlement of coral larval. Ecotoxicology 21: 1-8.

Kobluk DR and Lysenko MA. 1992. Storm features on a southern Caribbean fringing coral reef. SEPM Society for Sedimentary Geology 7(2): 213-221.

Kohn MH, Murphy WJ, Ostrander EA, Wayne RK. 2006. Genomics and conservation genetics. Trends in Ecology and Evolution 21(11): 629-637.

Krediet CJ, Ritchie KB, Cohen M, Lipp EK, Sutherland KP, Teplitski M. 2009. Utilization of mucus from the coral *Acropora palmata* by the pathogen *Serratia marcescens* and by environmental and coral commensal bacteria. Applied Environmental Microbiology 75(12): 3851-3858.

Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Marine Ecology Progress Series 323: 107-117.

Kuffner IB, Andersson AJ, Jokiel PL, Rodgers KS, Mackenzie FT. 2008. Decreased abundance of crustose coralline algae due to ocean acidification. Nature Geoscience 1(2): 114-117.

Kuntz NM, Kline DI, Sandin SA, Rohwer F. 2005. Pathologies and mortality rates caused by organic carbon and nutrient stressors in three Caribbean coral species. Marine Ecology Progress Series 294:173-180.

Lang JC. 2003. Caveats for the AGRRA “initial results” volume. Atoll Research Bulletin 496: xv-xx.

Langdon C and Atkinson MJ. 2005. Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. Journal of Geophysical Research 110: 16.

Lapointe BE, Barile PJ, Littler MM, Littler DS. 2005. Macroalgal blooms on southeast Florida coral reefs II. Cross-shelf discrimination of nitrogen sources indicates widespread assimilation of sewage nitrogen. Harmful Algae 4: 1106-1122.

Leichter JJ, Stewart HL, Miller SL. 2003. Episodic Nutrient Transport to Florida Coral Reefs. Limnology and Oceanography 48(4): 1394-1407.

Le Quéré C, Peters GP, Andres RJ, Andrew RM, Boden T, Ciais P, Friedlingstein P, Houghton RA, Marland G, Moriarty R, Sitch S, Tans P, Arneth A, Arvanitis A, Bakker DCE, Bopp L, Canadell JG, Chini LP, Doney SC, Harper A, Harris I, House JI, Jain AK, Jones SD, Kato E, Keeling RF, Klein Goldewijk K, Körtzinger A, Koven C, Lefèvre N, Omar A, Ono T, Park GH, Pfeil B, Poulter B, Raupach MR, Regnier P, Rödenbeck C, Saito S, Schwinger J, Segschneider J, Stocker BD, Tilbrook B, van Heuven S, Viovy N, Wanninkhof R, Wiltshire A, Zaehle S, Yue C. 2013. Global carbon budget 2013. Earth System Science Data Discussions 6(2):689-760.

Lesser M. 1997. Oxidative stress causes coral bleaching during exposure to elevated temperatures. Coral Reefs 16: 187-192.

Lesser M and Farrell J. 2004. Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. Coral Reefs 23: 367-377.

Lesser MP, Bythell JC, Gates RD, Johnstone RW, Hoegh-Guldberg O. 2007. Are infectious diseases really killing corals? Alternative interpretations of the experimental and ecological data. Journal of Experimental Marine Biology and Ecology. 346(1-2): 36-44.

Lesser M and Slattery M. 2011. Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. Biological Invasions 13(8): 1855-1868.

Levitan DR. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. Biological Bulletin 181(2): 261-268.

Lewis JB. 1977. Suspension feeding in Atlantic reef corals and the importance of suspended particulate matter as a food source. Proceedings of the 3rd International Coral Reef Symposium. pp. 405-408.

Lewis CF, Slade SL, Maxwell KE, Matthews TR. 2009. Lobster trap impact on coral reefs: Effects of wind-driven trap movement. New Zealand Journal of Marine and Freshwater Research 43: 271-282.

Lighty RG, MacIntyre IG, Stuckenrath R. 1982. *Acropora palmata* reef framework: A reliable indicator of sea level in the western Atlantic for the past 10,000 years. Coral reefs 1(2): 125-130.

Lirman D. 2000. Fragmentation in the branching coral *Acropora palmata* (Lamarck): growth, survivorship, and reproduction of colonies and fragments. Journal of Experimental Marine Biology and Ecology 251(1): 41-572.

Lirman D and Fong P. 1996. Susceptibility of coral communities to storm intensity, duration and frequency. Proceedings of the 8th International Coral Reef Symposium, Panamá 7: 561-566.

Lirman D and Fong P. 1997. Patterns of damage to the branching coral *Acropora palmata* following Hurricane Andrew: Damage and survivorship of hurricane-generated asexual recruits. Journal of Coastal Research 13: 67-72.

Lizama J and Blanquet RS. 1975. Predation on sea anemones by the amphinomid polychaete *Hermodice carunculata*. Bulletin of Marine Science 25: 442-443.

López-Victoria M and Zea S. 2004. Storm-mediated coral colonization by an excavating Caribbean sponge. Climate Research 26(3): 251-256.

Loya Y, Sakai K, Yamazato K, Nakano Y, Sembali H, van Woesik R. 2001. Coral bleaching: the winners and the losers. Ecology Letters 4: 122-131.

Lundgren I. 2008. The decline of elkhorn coral at Buck Island Reef National Monument: Protecting the first threatened coral species. Park Science 25: 36-43.

Maljković A, Leeuwen TE, Cove SN. 2008. Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. Coral Reefs, 27(3): 501.

Manzello DP, Kleypas JA, Budd DA, Eakin CM, Glynn PW, Langdon C. 2008. Poorly cemented coral reefs of the eastern tropical Pacific: Possible insights into reef development in a high-CO_2 world. Proceedings of the National Academy of Sciences 105(30): 10450-10455.

Mao-Jones J, Ritchie KB, Jones LE, Ellner SP. 2010. How microbial community composition regulates coral disease development. PLoS Biol 8(3): e1000345. doi:10.1371/journal.pbio.1000345.

Marsden JR. 1962. A coral-eating polychæte. Nature 193: 598.

Matthews HD and Caldeira K. 2008. Stabilizing climate requires near-zero emissions. Geophysical Research Letters 35(4): 5.

Mayer AG. 1914. The effect of temperature upon tropical marine animals. Carneige Institution of Washington Publication 183: 3-24.

Mayor PA, Rogers CS, Hillis-Starr ZM. 2006. Distribution and abundance of elkhorn coral, *Acropora palmata*, and prevalence of white-band disease at Buck Island Reef National Monument, St. Croix, US Virgin Islands. Coral Reefs 25(2): 239-242.

McCook LJ, Jompa J, Diaz-Pulido G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19(4): 400-417.

McWilliams JP, Cote IM, Gill JA, Sutherland WJ, Watkinson AR. 2005. Accelerating impacts of temperature-induced coral bleaching in the Caribbean. Ecology 86: 2055-2060.

Meyer E, Aglyamova GV, Wang S, Buchanan-Carter J, Abrego D, Colbourne JK, Willis BL, Matz MV. 2009. Sequencing and de novo analysis of a coral larval transcriptome using 454 GS-Flx. BMC Genomics 10(1): 219.

Miller AC. 1981. Cnidarian prey of the snails *Coralliophila abbreviata* and *C. caribaea* (Gastropoda: Muricidae) in Discovery Bay, Jamaica. Bulletin of Marine Science 31(4): 932-934.

Miller MW. 2001. Corallivorous snail removal: evaluation of impact on *Acropora palmata*. Coral Reefs 19(3): 293-295.

Miller MW and Williams DE. 2006. Coral disease outbreak Navassa, a remote Caribbean island. Coral Reefs 26: 97-101.

Miller M, Bourque A, Bohnsack J. 2002. An analysis of the loss of acroporid corals at Looe Key, Florida, USA: 1983-2000. Coral Reefs 21(2): 179-182.

Miller MW, Baums IB, Williams DE, Szmant AM. 2002. Status of Candidate coral, *Acropora palmata*, and its snail predator in the upper Florida Keys National Marine Sanctuary: 1998-2001. NOAA Technical Memorandum NMFS-SEFSC-479, Miami, FL. 26 pp.

Miller MW, Gleason A, McClellan D, Piniak G, Williams D, Wiener J, Gude A, Schwagerl J. 2008a. The State of Coral Reef Ecosystems of Navassa Island. In: Waddell JE, Clarke AM (eds) The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2008. NOAA Technical Memorandum NOS NCCOS 73. NOAA/NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team. Silver Spring, MD. Pp. 117-229.

Miller SL, Chiappone M, Rutten LM. 2007. 2007 Quick look report: Large-scale assessment of *Acropora* corals, coral species richness, urchins and *Coralliophila* snails in the Florida Keys National Marine Sanctuary and Biscayne National Park. Center for Marine Science, University of North Carolina-Wilmington, Key Largo, Florida. 147 pp. available at http://people.uncw.edu/millers/CoralReef_QuickLooks.htm

Miller SL, Chiappone M, Rutten LM, Swanson DW. 2008b. Population status of *Acropora* corals in the Florida Keys. Proceedings of the 11th International Coral Reef Symposium, pp. 775-779.

Minerals Management Service (MMS). 2006. The 5-Year Program: Encourage Development and Protect Resources. MMS Ocean Science. 3(2): 4.

Morgan MB and Snell TW. 2002. Characterizing stress gene expression in reef-building corals exposed to the mosquitocide dibrom. Marine Pollution Bulletin 44(11): 1206-1218.

Morgan M, Edge S, Snell T. 2005. Profiling differential gene expression of corals along a transect of waters adjacent to the Bermuda municipal dump. Marine Pollution Bulletin 51: 524-533.

Morris JA and Akins JL. 2009. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. Environmental Biology of Fishes 86: 389-398.

Mueller R, Tang JYM, Their R, Mueller JF. 2007. Combining passive sampling and toxicity testing for evaluation of mixtures of polar organic chemicals in sewage treatment plant effluent. Journal of Environmental Monitoring 9: 104-109.

Muller EM, Rogers CS, Spitzack AS, van Woesik R. 2008. Bleaching increases likelihood of disease on *Acropora palmata* (Lamarck) in Hawksnest Bay, St. John, US Virgin Islands. Coral Reefs 27(1): 191-195.

Mumby PJ, Hedley JD, Zychaluk K, Harborne AR, and Blackwell PG. 2006. Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: Fresh insights on resilience from a simulation model. Ecological Modelling 196(1-2): 131-148.

Mumby PJ, Hastings A, Edwards HJ. 2007a. Thresholds and the resilience of Caribbean coral reefs. Nature 450(7166): 98-101.

Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, Blackwell PG. 2007b. Trophic cascade facilitates coral recruitment in a marine reserve. Proceedings of the National Academy of Sciences (USA) 104: 8362-8367.

Mumby PJ. 2009. Herbivory versus corallivory: are parrotfish good or bad for Caribbean coral reefs? Coral Reefs 28(3): 683-690.

Mumby PJ, Harborne AR, Brumbaugh DR. 2011. Grouper as a natural biocontrol of invasive lionfish. PLoS ONE 6(6): e21510-e21510. doi: 10.1371/journal.pone.0021510.

NMFS (National Marine Fisheries Service). 1990. Recovery Priority Guidelines. 55 FR 24296.

NMFS. 2004. Listing Endangered and Threatened Wildlife and Plants and Designating Critical Habitat; 90-Day Finding on a Petition to List Elkhorn Coral, Staghorn Coral, and Fused-staghorn Coral. 69 FR 34995.

NMFS. 2006. Endangered and Threatened Species: Final Listing Determinations for Elkhorn Coral and Staghorn Coral. 71 FR 26852.

NMFS. 2008. Endangered and Threatened Species; Critical Habitat for Threatened Elkhorn and Staghorn Corals. 73 FR 72210.

NMFS. 2012. Endangered and Threatened Wildlife and Plants: Proposed Listing Determinations for 82 Reef-Building Coral Species; Proposed Reclassification of Acropora palmata and Acropora cervicornis from Threatened to Endangered. 77 FR 73220.

Negri AP and Heyward AJ. 2000. Inhibition of fertilization and larval metamorphosis of the coral *Acropora millepora* (Ehrenberg, 1834) by petroleum products. Marine Pollution Bulletin 41(7-12): 420-427.

Negri AP and Heyward AJ. 2001. Inhibition of coral fertilization and larval metamorphosis by tributyltin and copper. Marine Environmental Research 51(1): 17-27.

Negri AP, Smith LD, Webster NS, Heyward AJ. 2002. Understanding ship-grounding impacts on a coral reef: potential effects of anti-foulant paint contamination on coral recruitment. Marine Pollution Bulletin 44: 111-117.

Negri AP, Marshall PA, Heyward AJ. 2007. Differing effects of thermal stress on coral fertilization and early embryogenesis in four Indo Pacific species. Coral Reefs 26(4): 759-763.

Neigel JE and Avise JC. 1983. Clonal diversity and population structure in a reef-building coral, *Acropora cervicornis*: Self-recognition analysis and demographic interpretation. Evolution 37(33): 437-453.

Nieuwaal M. 2001. Requirements for sediment plumes caused by dredging. Department of Civil engineering, Section Hydraulics. Delft University of Technology, The Netherlands. p. 893.

Nystrom M, Folke C, Moberg F. 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends in Ecology and Evolution 15:413-417.

Oken L. 1915. Lehrbuch der Natureschichte 3 Tiel: Zoologie 1 Abth: Fleischlose Thiere 2 KL. 1 Zunft Erdkorallen. Steinkorallen: 59-74. Jena.

Omori M, Iwao K, Tamura M. 2008. Growth of transplanted *Acropora tenuis* 2 years after egg culture. Coral Reefs 27(1): 165-165.

Ostrander GK, Armstrong KM, Knobbe ET, Gerace D, Scully EP. 2000. Rapid transition in the structure of a coral reef community: the effects of coral bleaching and physical disturbance. Proceedings of the National Academy of Sciences 97: 5297-5302.

Ott B and Lewis JB. 1972. The importance of the gastropod *Coralliophila abbreviata* (Lamarck) and the polychaete *Hermodice carunculata* (Pallas) as coral reef predators. Canadian Journal of Zoology 50: 1651-1656.

Padilla C and Lara M. 1996. Efecto del tamano de las colonias en el crecimiento de *Acropora palmata* en Puerto Morelos, Quinta Roo, Mexico. Hidrobiologica (Iztapalapa) 6: 17-24.

Pait AS, Whitall DR, Jeffrey CFG, Caldow C, Mason AL, Christensen JD, Monaco ME, Ramirez J. 2007. An Assessment of Chemical Contaminants in the Marine Sediments of Southwest Puerto Rico. NOS NCCOS 52. Silver Spring, MD. NOAA/NOS/Center for Coastal Monitoring and Assessment. 116pp. Available at: http://www.ccma.nos.noaa.gov/publications/southwestpuertorico.pdf.

Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP. 2005. Are US coral reefs on the slippery slope to slime? Science 307(5716): 1725-1726.

Pandolfi JM and Jackson JBC. 2006. Ecological persistence interrupted in Caribbean coral reefs. Ecology Letters 9(7): 818-826.

Patterson KL, Porter JW, Ritchie KB, Polson SW, Mueller E, Peters EC, Santavy DL, Smith GW. 2002. The etiology of white pox, a lethal disease of the Caribbean elkhorn coral, *Acropora palmata*. Proceedings of the National Academy of Sciences 99: 8725-8730.

PBS&J. 2008. Best Management Practices (BMPs) for Construction, Dredge and Fill and Other Activities Adjacent to Coral Reefs. Prepared for the Southeast Florida Coral Reef Initiative (SEFCRI), Maritime Industry and Coastal Construction Impacts (MICCI) Focus Team, Local Action Strategy Project #6; the Florida Department of Environmental Protection (FDEP); and the NOAA Coral Reef Conservation Program (CRCP). Miami, FL. 126 pp.

Perez S and Weis V. 2006. Nitric oxide and cnidarian bleaching: an eviction notice mediates breakdown of a symbiosis. Journal of Experimental Biology 209: 2804-2810.

Peters EC. 1984. A survey of cellular reactions to environmental stress and disease in Caribbean scleractinian corals. Diseases of Marine Organisms 37: 1-4.

Peters EC, Oprandy JJ, Yevich PP. 1983. Possible causal agent of “white band disease” in Caribbean acroporid corals. Journal of Invertebrate Pathology 41(3): 394-396.

Peters EC, Halas JC, McCarty HB. 1986. Calicoblastic neoplasms in *Acropora palmata*, with a review of reports on anomalies of growth and form in corals. Journal of the National Cancer Institute 76(5): 895-912.

Peters EC, Gassman NJ, Firman JC, Richmond RH, Power EA. 1997. Ecotoxology of tropical marine ecosystems. Environmental Toxicology and Chemistry 16(1): 12–40.

Petersen D, Carl M, Borneman E, Brittsan M, Hagedorn M, Laterveer M, Schick M. 2008. Noah's Ark for the threatened elkhorn coral *Acropora palmata*. Coral Reefs 27(3): 715.

Pimentel, D, Zuniga R, Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52: 273-288.

Polson SW, Higgins JL, Woodley CM. 2009. PCR-based Assay for Detection of Four Coral Pathogens. Proceedings of the 11th International Coral Reef Symposium pp. 247-251.

Porter JW. 1976. Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. American Naturalist 110: 731-742.

Porter JW. 1987. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Florida): reef-building corals. Performed for Coastal Ecology Group, U.S. Army Corps of Engineers, Waterways Experiment Station and U.S. Department of the Interior, Fish and Wildlife Service, Research and Development, National Wetlands Research Center. TR EL-82-4. 23 pp.

Precht WF and Aronson RB. 2004. Climate flickers and range shifts of reef corals. Frontiers in Ecology and the Environment 2(6): 307-314.

Precht WF, Deslarzes K, Hickerson E, Schmahl GP, Sinclair J, Aronson R. 2008. Holocene Reef Development at The Flower Garden Banks: Recent Surprises. 11th International Coral Reef Symposium, Ft. Lauderdale, FL.

Randall CJ and Szmant AM. 2009. Elevated temperature affects development, survivorship, and settlement of the elkhorn coral, *Acropora palmata* (Lamarck 1816). Biological Bulletin 217: 269-282.

Rees JG, Setiapermana D, Sharp VA, Weeks JM, Martin Williams TM. 1999. Evaluation of the impacts of land-based contaminants on the benthic faunas of Jakarta Bay, Indonesia. Oceanologica Acts 22(6): 627-640.

Reichelt-Brushett AJ and Harrison PL. 2000. The effect of copper on the settlement success of larvae from the scleractinian coral *Acropora tenuis*. Marine Pollution Bulletin 41(7-12): 385-391.

Reichelt-Brushett AJ and Harrison PL. 2005. The effect of selected trace metals on the fertilization success of several scleractinian coral species. Coral Reefs 24(4): 524-534.

Renegar DA and Riegl BM. 2005. Effect of nutrient enrichment and elevated CO_2 partial pressure on growth rate of Atlantic scleractinian coral *Acropora cervicornis*. Marine Ecology Progress Series 293:69-76.

Rhyne A, Rotjan R, Bruckner A, Tlusty M. 2009. Crawling to collapse: Ecologically unsound ornamental invertebrate fisheries. PLoS ONE 4(12): e8413. doi:10.1371/journal.pone.0008413

Richmond RH and Hunter, CL. 1990. Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. Marine Ecology Progress Series 60: 185-203.

Richardson LL. 1999. *Coral Epidemiology*. Opportunities for Environmental Applications of Marine Biology. Proceedings of the October 5-6, 1999, Workshop. WHOI-R-99-00: 112-125.

Ridley SO. 1884. On the classificatory value of growth and budding in the Madreporidae, and on a new genus illustrating this point. American Magazine of Natural History 13:284–291.

Ritchie KB and Smith GW. 1995. Preferential carbon utilization by surface bacterial communities from water mass, normal, and white-band diseased *Acropora cervicornis*. Molecular Marine Biology and Biotechnology 4(4): 345-352.

Ritchie KB and Smith GW. 1998. Type II white-band disease. Revista De Biologia Tropical 46: 199-203.

Ritchie KB, Polson SW, Smith GW. 2001. Microbial disease causation in marine invertebrates: problems, practices, and future prospects. Hydrobiologia 460: 131-139.

Ritchie K. 2006. Regulation of microbial populations by coral surface mucus and mucus-associated bacteria. Marine Ecology Progress Series 322: 1-14.

Ritson-Williams R, Paul VJ, Arnold SN, Steneck RS. 2010. Larval settlement preferences and post-settlement survival of the threatened Caribbean corals *Acropora palmata* and *A. cervicornis*. Coral Reefs 29(1): 71-81.

Rocha LA, Robertson DR, Rocha C, Van Tassell JL, Craig MT, Bowen BW. 2005. Recent invasion of the tropical Atlantic by an Indo-Pacific coral reef fish. Molecular Ecology 14(13): 3921-3928.

Rodriguez-Martinez RE, Banaszak AT, Jordan-Dahlgren E. 2001. Necrotic patches affect *Acropora palmata* (Scleractinia: Acroporidae) in the Mexican Caribbean. Diseases of Aquatic Organisms 47(3): 229-234.

Rogers CS. 1979. The effect of shading on coral reef structure and function. Journal of Experimental Marine Biology and Ecology 41(3): 269-288.

Rogers CS. 1983. Sublethal and lethal effects of sediments applied to common Caribbean reef corals in the field. Marine Pollution Bulletin 14: 378-382.

Rogers CS. 1990. Responses of coral reefs and reef organisms to sedimentation. Marine Ecology Progress Series 62: 1-2.

Rogers CS, Suchanek TH, Pecora FA. 1982. Effects of Hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, U.S. Virgin Islands. Bulletin of Marine Science, 32, 532-548.

Rogers CS, Sutherland KP, Porter JW. 2005. Has white pox disease been affecting *Acropora palmata* for over 30 years? Coral Reefs 24(2): 194-194.

Rogers CS et al. 2008. Ecology of Coral Reefs in the U.S. Virgin Islands. In: Riegl B and Dodge RE (Eds.). Coral Reefs of the USA. Coral Reefs of the World Volume 1. Springer. pp. 303-374.

Rogers CS and Muller EM. 2012. Bleaching, disease and recovery in the threatened scleractinian coral *Acropora palmata* in St. John, US Virgin Islands: 2003–2010. Coral Reefs. doi: 10.1007/s00338-012-0898-8.

Rosenberg E, Koren O, Reshef L, Efrony R, Zilber-Rosenberg I. 2007. The role of microorganisms in coral health, disease and evolution. Nature Reviews Microbiology 5: 355-362.

Rutzler, K. 2002. Impact of crustose clionid sponges on Caribbean reef corals. Acta Geologica Hispanica 37:61-72.

Rypien KL. 2008. The origins and spread of *Aspergillus sydowii*, an opportunistic pathogen of Caribbean gorgonian corals. A Dissertation Presented to the Faculty of the Graduate School of Cornell University. 113 pp.

Sammarco PW. 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. Journal of Experimental Marine Biology and Ecology 45(2-3): 245-272.

Sammarco PW. 1985. The Great Barrier Reef versus the Caribbean: comparisons of grazers, coral recruitment patterns and reef recovery. Proceedings of the 5th International Coral Reef Symposium 4: 391-97.

Sammarco PW and Carleton JH. 1982. Damselfish territoriality and coral community structure: reduced grazing, coral recruitment, and effects on coral spat. Proceedings of the 4th International Coral Reef Symposium 2: 525-536.

Santavy DL and Peters EC. 1997. Microbial pests: coral disease in the western Atlantic. Proceedings of the 8th International Coral Reef Symposium, Panama. Pp. 607-612.

Schärer M, Nemeth M, Valdivia A, Miller M, Williams D, Diez C. 2009. Elkhorn coral distribution and condition throughout the Puerto Rican Archipelago. Proceedings of the 11th International Coral Reef Symposium pp. 815-819.

Schneider K and Erez J. 2006. The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystoma*. Limnology and Oceanography 51(3): 1284-1293.

Schwarz JA, Brokstein P, Manohar C, Coffroth MA, Szmant AM, Medina M. 2006. Coral Reef Genomics: Developing tools for functional genomics of coral symbiosis. Proceedings of the 10th International Coral Reef Symposium. Pp. 274-281.

Schwarz JA, Brokstein PB, Voolstra C, Terry AY, Szmant A, Coffroth MA, Miller DJ, Medina M. 2008. Coral life history and symbiosis: functional genomic resources for two reef building Caribbean corals, *Acropora palmata* and *Montastraea faveolata*. BMC Genomics 9: 97.

Scully NM, Maie N, Dailey SK, Boyer JN, Jones RD, Jaffe R. 2004. Early diagenesis of plant-derived dissolved organic matter along a wetland, mangrove, estuary ecotone. Limnology and Oceanography 49(5): 1667-1678.

Shinn EA. 1963. Spur and groove formation on the Florida Reef Tract. Journal of Sediment Petrology 33: 291-303.

Shinn EA. 1966. Coral growth-rate: An environmental indicator. Journal of Paleontology 40: 233-240.

Shinn EA. 1976. Coral reef recovery in Florida and the Persian Gulf. Environmental Geology 1: 241-254.

Shinn EA, Smith GW, Prospero JM, Betzer P, Hayes ML, Garrison V, Barber RT. 2000. African Dust and the Demise of Caribbean Coral Reefs. Geophysical Research Letters 27(19): 3029-3032.

Shinn EA, Griffin DW, and Seba DB. 2003. Atmospheric transport of mold spores in clouds of desert dust. Archives of Environmental Health 58:498-504.

Silverman J, Lazar B, Cao L, Caldeira K, Erez J. 2009. Coral reefs may start dissolving when atmospheric CO_2 doubles. Geophysical Research Letters 36: 5.

Simpson MC, Scott D, New M, Sim R, Smith D, Harrison M, Eakin CM, Warrick R, Strong AE, Kouwenhoven P, Harrison S, Wilson M, Nelson GC, Donner S, Kay R, Geldhill DK, Liu G, Morgan JA, Kleypas JA, Mumby PJ, Christensen TRL, Baskett ML, Skirving WJ, Elrick C, Taylor M, Bell J, Rutty M, Burnett JB, Overmas M, Robertson R, Stager H. 2009. An Overview of Modeling Climate Change

Impacts in the Caribbean Region with contribution from the Pacific Islands, United Nations Development Programme (UNDP), Barbados, West Indies.

Slomp, CP and P Van Cappellen. 2004. Nutrient inputs to the coastal ocean through submarine groundwater discharge: controls and potential impact. Journal of Hydrology 295 (1-4): 64-86.

Smith SH. 1988. Cruise ships: a serious threat to coral reefs and associated organisms. Ocean Shoreline Management 11: 231-248.

Soong K and Lang JC. 1992. Reproductive integration in reef corals. Biological Bulletin 183(3): 418-431.

Stabenau ER, Zepp RC, Bartels E, Zika RG. 2004. Role of seagrass *Thalassia testudinum* as a source of chromophoric dissolved organic matter in coastal south Florida. Marine Ecology Progress Series 282: 59-72.

Stanley GD. 2006. Photosymbiosis and the evolution of modern coral reefs. Science 312(5775): 857-858.

Steneck RS. 1986. The ecology of coralline algal crusts: Convergent patterns and adaptative strategies. Annual Review of Ecology and Systematics 17: 273-303.

Stoddart DR. 1962. Catastrophic storm effects on the British Honduras reefs and cays. Nature 196: 512-514.

Stoddart DR. 1969. Post-hurricane changes in British Honduras reefs and cays. Atoll Research Bulletin 131: 1-25.

Stone L, Huppert A, Rajagopalan B, Loya Y. 1999. Mass coral reef bleaching: a recent outcome of increased El-Nino activity? Ecology Letters 2:325-330.

Stumpp M, Wren J, Melzner F, Thorndyke MC, Dupont ST. 2011. CO_2 induced seawater acidification impacts sea urchin larval development I: Elevated metabolic rates decrease scope for growth and induce developmental delay. Comparative Biochemistry and Physiology, Part A 160(3): 331-340.

Suchanek TH and Green DJ. 1981. Interspecific competition between *Palythoa caribaeorum* and other sessile invertebrates on St. Croix Reefs, U.S. Virgin Islands. Proceedings of the Fourth International Coral Reef Symposium, Manila. 2: 679-684.

Sussman M, Loya Y, Fine M, Rosenberg E. 2003. The marine fireworm *Hermodice carunculata* is a winter reservoir and spring-summer vector for the coral-bleaching pathogen *Vibrio shiloi.* Environmental Microbiology 5(4): 250-255.

Suter GW. 2006. Ecological risk assessment and ecological epidemiology for contaminated sites. Human and Ecological Risk Assessment 12: 31-38.

Suter GW, Cormier SM, Norton S. 2007. Ecological epidemiology and causal analysis. Ecological Risk Assessment. Pp. 39-68.

Sutherland KP, Porter JW, Turner JW, Thomas BJ, Looney EE, Luna TP, Meyers MK, Futch JC, Lipp EK. 2010. Human sewage identified as likely source of white pox disease of threatened Caribbean elkhorn coral*, Acropora palmata*. Environmental Microbiology 12: 1122-1131.

Sutherland KP, Shaban S, Joyner JL, Porter JW, Lipp EK. 2011. Human pathogen shown to cause disease in the threatened elkhorn coral *Acropora palmata*. PLoS ONE 6(8): e23468. doi:10.1371/journal.pone. 0023468

Szmant AM. 1986. Reproductive ecology of reef corals. Coral Reefs 5: 43-54.

Szmant AM. 2002. Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? Estuaries 25(4): 743-766.

Szmant AM and Miller MW. 2005. Settlement preferences and post-settlement mortality of laboratory cultured and settled larvae of the Caribbean hermatypic corals *Montastraea faveolata* and *Acropora palmata* in the Florida Keys, USA. Proceedings of the 10th International Coral Reef Symposium 1: 43-49.

Talge H. 1991. Impact of recreational divers on scleractinian corals of the Florida Keys. M.Sc. Thesis, University of South Florida, St. Petersburg, USA, p. 92.

Tanzil JTI, Brown BE, Tudhope AW, Dunne RP. 2009. Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between 1984 and 2005. Coral Reefs 28(2): 519-528.

Tarrant AM, Atkinson MJ, Atkinson S. 2004. Effects of steroidal estrogens on coral growth and reproduction. Marine Ecology-Progress Series 269: 121-129.

Teplitski M and Ritchie KB. 2009. How feasible is biological control of coral diseases? Trends in Ecology and Evolution 24(7): 378-385.

Thresher RE. 1976. Field Analysis of the Territoriality of the Threespot Damselfish, *Eupomacentrus planifrons* (Pomacentridae). Copeia 1976(2): 266-276.

Thursfield M. 2007. Veterinary Epidemiology. 3rd edition. Blackwell Publishing, Ames Iowa.

Tomascik T and Sander F. 1987. Effects of eutrophication on reef-building corals. II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. Marine Biology 945: 53-75.

Tougas JI and Porter JW. 2002. Differential coral recruitment patterns in the Florida Keys. In: Porter JW and Porter KG (eds.) The Everglades, Florida Bay, and Coral Reefs of the Florida Keys, An Ecosystem Sourcebook. CRC Press, Boca Raton, FL. pp. 789-811.

Trapido-Rosenthal H, Zielke S, Owen R, Buxton L,Boeing B, Bhagooli R, Archer J. 2005. Increased zooxanthellae nitric oxide synthase activity is associated with coral bleaching. Biological Bulletin 208: 3-6.

Tratalos JA and Austin TJ. 2001. Impacts of recreational SCUBA diving on coral communities of the Caribbean island of Grand Cayman. Biological Conservation 102(1): 67-75.

Trenberth KE and Shea DJ. 2006. Atlantic hurricanes and natural variability in 2005. Geophysical Research Letters 33(12): L12704.

Tunnicliffe V. 1981. Breakage and propagation of the stony coral *Acropora cervicornis.* Proceedings of the National Academy of Sciences 78(4): 2427-2431.

U.S. Fish and Wildlife Service. 2004. Investigations of Mitigation for Coral Reef Impacts in the U.S. Atlantic: South Florida and the Caribbean. Final Report. U.S. Fish and Wildlife Service, Southeast Region. Atlanta, GA. September 2004. 53pp + App.

van Hooidonk R, Maynard JA, Planes S. 2013. Temporary refugia for coral reefs in a warming world. Nature Climate Change. doi:10.1038/nclimate1829.

Van Veghel MLJ and Hoetjes PC. 1995. Effects of tropical storm Bret on Curacao reefs. Bulletin of Marine Science 56(28): 692-694.

Vardi T. 2011. The threatened Atlantic elkhorn coral, *Acropora palmata*: population dynamics and their policy implications. PhD dissertation, University of California, San Diego. 145 pp.

Vargas-Angel B, Thomas JD, Hoke SM. 2003. High-latitude *Acropora cervicornis* thickets off Fort Lauderdale, Florida, USA. Coral Reefs 22(4): 465-473.

Vaughn TW. 1915. The geological significance of the growth rate of the Floridian and Bahamian shoal-water corals. Journal of the Washington Academy of Science 5: 591-600.

Vaughan TW. 1918. The temperature of the Florida coral-reef tract. Papers from the Department of Marine Biology Carnegie Institution of Washington 9: 319-339.

Veron JEN. 1986. Corals of Australia and the Indo-Pacific. UNSW Press, Sydney. 644 pp.

Veron JEN. 1995. Corals in space and time. UNSW Press, Sydney.

Veron JEN. 2000. Corals of the World. Australian Institute of Marine Science, Townsville, Australia.

Veron JEN, Hoegh-Guldberg O, Lenton TM, Lough JM, Obura DO, Pearce-Kelly P, Sheppard CRC, Spalding M, Stafford-Smith MG, Rogers AD. 2009. The coral reef crisis: The critical importance of <350 ppm CO2. Marine Pollution Bulletin 58(10): 1428-1436.

Vijayavel K, Downs CA, Ostrander GK, Richmond RH. 2012. Oxidative DNA damage induced by iron chloride in the larvae of the lace coral *Pocillopora damicornis*. Comparative Biochemistry and Physiology Part C: Toxicology and Pharmacology 155: 275-280.

Vizel M, Loya Y, Downs CA, Kramarsky-Winter E. 2011. A novel method for coral explant culture and micropropagation. Marine Biotechnology 13: 423-432.

Vollmer SV and Palumbi SR. 2002. Hybridization and the evolution of reef coral diversity. Science 296: 2023-2025.

Vollmer SV and Palumbi SR. 2007. Restricted gene flow in the Caribbean staghorn coral *Acropora cervicornis*: Implications for the recovery of endangered reefs. Journal of Heredity 98(1): 40-50.

Vollmer SV and Kline DI. 2008. Natural disease resistance in threatened staghorn corals. PLoS ONE 3(11): e3718. doi:10.1371/journal.pone.0003718.

Waddell JE (ed.). 2005. The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2005. NOAA Technical Memorandum NOS NCCOS 11. NOAA/NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team, Silver Spring, MD. 522 pp.

Waddell JE and Clark AM (ed.). 2008. The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2008. NOAA Technical Memorandum. NOAA/NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team, Silver Spring, MD.

Weil E, Urreiztieta I, Garzon-Ferreira J. 2002. Geographic variability in the incidence of coral and octocoral diseases in the wider Caribbean. Proceedings of the 9th International Coral Reef Symposium Bali, 23-27 October 2000, 2: 1231-1237.

Weir-Bush JR, Garrison VH, Smith GW, Shinn EA. 2004. The relationship between gorgonian coral (Cnidaria: Gorgonacea) diseases and African dust storms. Aerobiologia 20:119-126.

Weis VM, Davy SK, Hoegh-Guldberg O, Rodriguez-Lanetty M, Pringe JR. 2008. Cell biology in model systems as the key to understanding corals. Trends in Ecology and Evolution 23(7): 369-376.

Wells JW. 1933. A study of the reef Madreporaria of the Dry Tortugas and sediments of coral reefs. Unpublished manuscript. Cornell Univ., Ithaca NY. 138 pp.

Wells JW. 1957. Coral reefs In: Hedgepeth (ed) Treatsie on marine ecology and paleoecology 1 Ecology. Geo Soc Amer Mem 67: 609-631

Wheaton JW and Jaap WC. 1988. Corals and other prominent benthic cnidaria of Looe Key National Marine Sanctuary, FL. Florida Marine Research Publication 43.

Whelan KRT, Miller J, Sanchez O, Patterson M. 2007. Impact of the 2005 coral bleaching event on *Porites porites* and *Colpophyllia natans* at Tektite Reef, U.S. Virgin Islands. Coral Reefs 26(3): 689-693.

Wilkinson C (Ed.). 2000. Status of Coral Reefs of the World: 2000. Global Coral Reef Monitoring Network and Australian Institute of Marine Science. Townsville, Australia.

Wilkinson C (Ed.). 2004. Status of Coral Reefs of the World: 2004. Global Coral Reef Monitoring Network and Australian Institute of Marine Science. Townsville, Australia. 557pp.

Wilkinson CL and Souter D. 2008. Status of Caribbean coral reefs after bleaching and hurricanes in 2005. Global Coral Reef Monitoring Network, and Reef and Rainforest Research Centre. Townsville, Australia. 152 pp.

Williams DE and Miller MW. 2005. Coral disease outbreak: pattern, prevalence, and transmission in *Acropora cervicornis*. Marine Ecology Progress Series 301: 119-128.

Williams DE and Miller MW. 2006. Importance of disease and predation to the growth and survivorship of juvenile *Acropora palmata* and *Acropora cervicornis*: A demographic approach. Proceedings of the 10th International Coral Reef Symposium. Pp. 1096-1104.

Williams DE and Miller MW. 2010. Stabilization of fragments to enhance asexual recruitment in *Acropora palmata*, a threatened Caribbean coral. Restoration Ecology 18(S2): 446-451.

Williams DE, Miller MW. 2012. Attributing mortality among drivers of population decline in *Acropora palmata* in the Florida Keys (USA). Coral Reefs 31: 369-382.

Williams DE, Miller MW, Kramer KL. 2008. Recruitment failure in Florida Keys *Acropora palmata*, a threatened Caribbean coral. Coral Reefs 27: 697-705.

Williams ID, Polunin NVC, Hendrick VJ. 2001. Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. Marine Ecology Progress Series 222: 187-196.

Wobeser GA. 1981. Diseases of Wild Waterfowl. New York: Plenum Press.

Wobeser GA. 1994. Investigation and management of disease in wild animals. New York, USA. 264 p.

Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe VJ, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Niegel J, Sides EM. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science 214: 749-755.

Woodley CM, Downs CA, Fauth JE, Mueller E, Halas JC, Bemiss J, Ben-Haim Y, Rosenberg E. 2002. A novel diagnostic system to assess the physiological status of corals. Proceedings of the Ninth International Coral Reef Symposium, Bali, 23-27 October 2000 2: 1267-1272.

Woodley CM, Bruckner AW, McLenon AL, Higgins JL, Galloway SB, Nicholson JH. 2008. Field Manual for Investigating Coral Disease Outbreaks. NOAA Technical Memorandum NOS NCCOS 80 and CRCP 6. National Oceanic and Atmospheric Administration, Silver Spring, MD 85pp.

Wooldridge SA. 2009. Water quality and coral bleaching thresholds: Formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. Marine Pollution Bulletin 58: 745-751.

Work TM and Aeby GS. 2006. Systematically describing gross lesions in corals. Diseases of Aquatic Organisms 70: 155-160.

Work TM, Richardson LL, Reynolds TL, Willis BL. 2008. Biomedical and veterinary science can increase our understanding of coral disease. Journal of Experimental Marine Biology and Ecology 362:63-70.

Young OR, Osherenko G, Ekstrom J, Crowder LB, Ogden J, Wilson JA, Day JC, Douvere F, Ehler CN, McLeod K, Peach R. 2007. Solving the Crisis in Ocean Governance: Place-Based Management of Marine Ecosystems. Environment 49(4): 20-32.

Zea S and Weil E. 2003. Taxonomy of the Caribbean excavating sponge species complex *Cliona caribbaea –C. aprica – C. langae* (Porifera, Hadromerida, Clionaidae). Caribbean Journal of Science 39(3): 348–370.

Zea S, Geister J, Garzon-Ferreira J, Diaz JM. 1998. Biotic changes in the reef complex of San Andres (southwestern Caribbean Sea, Colombia) occurring over three decades. Atoll Research Bulletin 456: 1-30.

Zimmer B, Precht W, Hickerson E, Sinclair J. 2006. Discovery of *Acropora palmata* at the Flower Garden Banks National Marine Sanctuary, northwestern Gulf of Mexico. Coral Reefs 25: 192.

Zoller U. 2008. Distribution profiles of endocrine disrupting PAHs/APEOs in river sediments: is there a potential ecotoxicological problem? Water Science and Technology 57(2): 237-242.

APPENDIX A

Summary of trade and collection laws for individual Caribbean nations

INTERNATIONAL TRADE IN CORAL AND CORAL REEF SPECIES: THE ROLE OF THE UNITED STATES, Report of the Trade Subgroup of the International Working Group to the U.S. Coral Reef Task Force March 2, 2000. Washington, D.C.

Country	Law/Prohibition	Citation
U.S. Federal Waters (South Atlantic, Gulf of Mexico, and Caribbean)		
Fishery Management Plans for: Coral and Coral Reefs of the Gulf of Mexico and South-Atlantic, April 1982, with Amendment 2 & 3 (1994-1995) and Corals and Reef Associated Plants and Invertebrates of Puerto Rico and the U.S. Virgin Islands, July 1994 *(Implemented at 50 C.F.R. Part 622)*	**Regulations relating to Coral/Live Rock** <u>Gulf of Mexico and South Atlantic EEZ</u> Prohibits harvest or possession of wild live rock in the Gulf or South Atlantic EEZ after 1997, with an exception for aquacultured live rock if taken under permit. Prohibits harvest of Gulf and South Atlantic or Caribbean prohibited coral (listed in appendix, includes all corals in the Class Hydrozoa and Class Anthozoa), with an exception for scientific and educational purposes by permit. Foreign fishing of corals is prohibited. The direct take of stony corals and sea fans and the destruction of corals in prohibited. Corals taken incidentally in association with other fisheries must be returned to area of capture. <u>Caribbean EEZ</u> Prohibits take or possession of Caribbean prohibited coral (listed in Appendix) from the Caribbean EEZ Harvest and possession of stony corals, octocorals, and live rock, whether dead or alive, are prohibited, except for the purpose of scientific research, education, and restoration. Prohibits sale or purchase of Caribbean prohibited coral harvested in the Caribbean EEZ. Items will be presumed to be harvested in the Caribbean EEZ unless accompanied by documentation showing it was harvested elsewhere. Harvest and possession of any species, if attached to live rock, is prohibited. Harvest or possession of reef-associated invertebrates requires a permit. **Regulations relating to Aquarium Marine Fish** <u>Caribbean EEZ</u> Prohibits fishing or possession of Caribbean prohibited coral (listed in appendix) and certain	50 C.F.R. §§ 622.42(b); 622.43(a)(2)(ii); 622.33(b)(4)(iv) 50 C.F.R. § 622.4(a)(1),(3) 50 C.F.R. § 622.32(b)(2) 50 C.F.R. § 622.32(b)(1) 50 C.F.R. § 622.45(a) 50 C.F.R. § 622.32(b)

Country	Law/Prohibition	Citation
FMPs for South Atlantic, Gulf and Caribbean EEZs *(Cont'd)*	fish (foureye, banded, and longsnout butterfly fish; jewfish; Nassau grouper; and seahorses). Authorizes harvest of marine aquarium fish in the Caribbean EEZ only by a hand-held dip net or a hand-held slurp gun **Destructive Fishing Practices** <u>Caribbean, Gulf or South Atlantic EEZ</u> Prohibits use of explosive, poison or toxic chemicals for fishing in the Caribbean, Gulf, or South Atlantic EEZ	50 C.F.R. § 622.41(b) 50 C.F.R. § 622.31(a),(b), (e)
U.S. State/Territorial Waters		
Puerto Rico[5]	**Laws and Regulations relating to Coral** Prohibits extracting, removing, mutilating or in any other way destroying or damaging any coral reef or coraline community or part of these. Prohibits offering for sale, exchange, donation or to in any other way traffic or dispose of a coral reef alive or dead or part of this alive or dead. Habitats associated with coral reefs, such as seagrasses, are afforded the same protection as coral resources. **Laws/Regulations relating to Marine Fish** Regulates commercial and recreational fishing activities and gear, marine life collection and export, scientific collection, exhibition and educational activities, and importation of organisms for aquaculture.	P.R. Law No. 147 P.R. Law No. 278 and Fishing Regulation 6768 (as amended)
Florida[6]	**Laws/Regulations relating to Coral/Live Rock** Prohibits the take/attempted take, destruction, sale/attempted sale or possession of sea fan of the species *Gorgonia flabellum* or *Gorgonia ventalina*, any hard or stony coral (Order Scleractinia) or any fire coral (Genus Millepora) harvested with state waters Prohibits harvest of live rock in state waters; permits harvest of aquacultured live rock Prohibits destruction, damage, removal or taking of coral and rock of the John Pennekamp Coral Reef State Park	Florida Admin. Code Ann. 68B-42.009(1) Fla. Admin. Code Ann. R. 68B-42.008 Fla. Stat. Ann. § 258.083

[5] The Puerto Rico section of the table was updated to reflect changes in Puerto Rico legislation, and to correct inaccuracies.
[6] The Florida section of the table was updated to reflect changes in Florida state legislation, and to correct inaccuracies.

Country	Law/Prohibition	Citation
Florida *(Cont'd)*	Prohibits harvest, possession or landing of more than 6 octocoral colonies per day in state waters for recreational harvest	Fla. Admin. Code Ann. r. 68B-42.005(4)
	No bag limits for commercial harvest of octocorals	Fla. Admin. Code Ann. r. 68B-42.006(2)(e)
	Requires additional endorsement to sell to a wholesale dealer species of saltwater products that are designated as restricted by the state	Fla. Stat. Ann. § 370.01(23) & 370.06(2)(b)(1)
	Requires tropical marine ornamentals to be landed alive and have onboard a vessel a continuously circulating live well or aeration or oxygenation system of adequate size and capacity to maintain the organisms	Fla. Admin. Code Ann. r. 68B-42.0035
	Prohibits harvest, possession or landing of more than 20 individuals per day of tropical ornamental marine fish species and no more than one gallon per day of tropical marine plants	Fla. Admin. Code Ann. r. 68B-42.005(1)&(2)
	Prohibits import or possession of marine plant or animal not indigenous to Florida which may endanger or infect the marine resources of the state or pose a human health hazard	F.S.A. § 370.081(1)
	Laws/Regulations relating to Aquarium Marine Fish	
	Prohibits importation of sea snakes, weeverfish & stonefishes	F.S.A. § 370.081(2)
	Sets commercial harvest season for tropical ornamental marine species and commercial bag limits for angelfish, butterflyfish, porkfish and hogfish	Fla. Admin. Code Ann. r. 68B-42.006(2)
	Prohibits harvest or possession of certain angelfish, butterflyfish, gobies, jawfishes, porkfish, and hogfish species under certain sizes in state waters	Florida Code Annotated 68B-42.004
	Prohibits harvest, possession or landing of more than 5 angelfishes per day in state waters	Fla. Admin. Code Ann. r. 68B-42.005(3)
	Sets commercial bag limit of 400 "pink-tipped" anemones (Genus *Condylactus*) per vessel per day; one gallon of starsnails (*Lithopoma americanum* or *Australium phoebium*) per person per day; and one quart of blue-legged or tricolor hermit crabs *(Clibanarius tricolor)* per person or per vessel each day	Fla. Admin. Code Ann. r. 68B-42.006(2)(f)-(h)
U.S. Virgin Islands	**Laws relating to Coral/ Live Rock**	
	Unlawful to take, catch, possess, injure, harass, kill, or attempt to take, catch, possess, injure, harass or kill, or sell or offer for sale, or	12 V.I.C. § 105 (a)

Country	Law/Prohibition	Citation
	transport or export, whether or not for sale, any indigenous species, including live rock; exception for valid fishing or hunting licenses, scientific or aquarium collecting permits, or indigenous species retention permits.	
	Harvest of live rock and all corals for commercial and recreational purposes is prohibited without a permit. Permits to collect specimens of marine life forms, including live rock, whether or not for sale, and whether or not intended for shipment or export, are authorized for: (A) A private aquarist collecting for a personal aquarium of not more than fifty (50) gallons capacity; (B) A person maintaining an aquarium of any size for a commercial purpose; and (C) A collector for shipment, export, and sale.	12 V.I.C. § 106(c)(1)
	Permits for coral and live rock are provided on a onetime, case-by-case basis, and require submission of species name and number, location of activity, capture methods, and holding facilities.	12 V.I.C. § 906(a)(7)
	A permit is required for the harvest and export of other invertebrates for the marine aquaria trade; 53 permits were issued 1990-1994.	
	Prohibits taking of sand, rock, mineral, marine growth and coral (including black coral), natural materials, or other natural products of the sea, excepting fish and wildlife, from the shorelines without first obtaining a coastal zone permit.	
Caribbean/Central American Countries		
Bahamas	Coral Trade and Protection Bans collecting of corals; bans export of marine products by non-Bahamians	Fisheries Resources Regulations, 1986
	Bans take of fish, turtle, crawfish, conch, and welks in national parks; or destruction or removal of any animals, including coral, bans removal of sand in national parks	Bahamas National Trust Act, 1959
	Destructive Fishing Practices Prohibits use of bleach, poisons or explosives	Fisheries Resources Regulations, 1986
Belize	Coral Trade and Protection Protects coral reefs within areas designated as national Parks	National Park System Act, 1981
Bermuda	Coral Trade and Protection Prohibits take of coral, flora and fauna in coral reef preserves; regulates take of spiny lobsters, fish, scallops, turtles	Coral Reef Preserves Act, 1966; Fisheries Regulation 1972
	Destructive Fishing Practices	

Country	Law/Prohibition	Citation
	Prohibits use of explosives	Fisheries Regulations, 1972
British Virgin Islands	Coral Trade and Protection Provides for protection of coral reefs in marine parks and protected areas	Marine Parks and Protected Areas Ordinance, 1979
Cayman Islands	Coral Trade and Protection Controls take of spiny lobsters, conch, coral, and shells	Marine Conservation Law, 1978
Cuba	Coral Trade and Protection Controls take of conch	Legislation, 1977
Dominican Republic	Coral Trade and Protection Controls take of coral	Ley 1728, 1976
Guadalupe	Coral Trade and Protection Controls take of turtles, spiny lobster, and coral	Legislation, 1979
Honduras	Coral Trade and Protection Declares coral reefs as protected areas	Ley de Pescar, 1959
Jamaica	Coral Trade and Protection Protects black coral, turtles, and other marine species Destructive Fishing Practices Prohibits fishing with poison or explosives	Wildlife Protection Law, 1945
Mexico	Coral Trade and Protection Bans collection of *plexaura homomalla* Requires export and import permit for corals, issued by the National Institute of Ecology	Decree 1974 Agreement Establishing the Classification and Codification of Goods Whose Importation and Exportation are Subject to regulation by the Secretariat of the Environment, Natural Resources and Fisheries (9/22/97)
Netherland Antilles	Coral Trade and Protection Controls take of spiny lobster, take of turtles eggs, and collection or destruction of coelenterates and crustose coralline algae Bans collection and destruction of coelenterates and crustose coralline algae Bans coral collection	Bonaire, the Marine Environment Ordinance, 1985 Curacao – the Reef Management Ordinance, 1976 Aruba
St. Lucia	Coral Trade and Protection Prohibits sale and export of aquarium fish; protects turtles and corals; controls take of conch Destructive Fishing Practices Prohibits dynamiting of coral reefs	Fisheries legislation Wildlife Protection Ordinance, 1980

APPENDIX B

Glossary

Acclimatization within the adaptive physiological limits (genotype) of an organism, there can be short-term responses or adjustments of an individual to exposures to different or changing natural environments.

Acclimation is the physiologic adjustment to a new environment in the laboratory, versus acclimatization is the physiologic adjustment to a new environment in the natural environment.

Accretion growth by external addition of new matter.

Adaptation is any heritable behavioral, morphological, or physiological trait that maintains or increases the fitness of an organism to live under a given set of environmental conditions. Adaptation, measured as fitness of the organism, is the result of natural selection.

The adaptation of an organism to its environment is exhibited by its ability to function between some upper and lower limits in a range of environmental conditions.

The key to adaptation is the genetic variability of local populations that exist under particular environments and have evolved genetic adaptations to them. Genetic diversity and phenotypic plasticity, the physical expression of the interaction between genotype and the environment, within a population enable individuals to respond to short-term or long-term changes in the environment.

Allee effect the reduced likelihood of finding a mate resulting from low population densities.

Allorecognition immunoresponse process by which an organism recognizes self versus non-self.

Allozyme variant of an enzyme coded by a different allele.

Aragonite a mineral identical in chemical composition with calcite or carbonate of lime, but differing from it in its crystalline form and some of its physical characters.

Axial relating to or parallel with the long axis of a coral polyp.

Beach nourishment a technique used to restore an eroding or lost beach, involving placing appropriately sourced sand on the shoreline to widen the beach, for the purpose of protecting adjoining natural and man-made assets.

Biocriteria narrative descriptions or numerical values that are used to describe the reference condition of aquatic biota inhabiting waters of a designated aquatic life use.

Bleaching when physically stressed coral polyps expel their algal cells (zooxanthellae) and the coral colony takes on a stark white appearance.

Broadcast spawner	A form of sexual reproduction in which eggs and sperm are released usually during mass spawning events once a year, a few nights after full moon. The gametes drift to the water surface where fertilization occurs. After a few days, the embryos will have developed into coral larvae.
Brooding coral	coral which harbors or broods developing larvae within its polyps.
Calicoblastic epidermis	outer layer of cells (epidermis) lying against the calcifying skeleton.
Calicoblastic epitheliomas	an abnormal new mass of tissue; or neoplasm.
Cyanobacteria	also known as blue-green algae; predominantly photosynthetic prokaryotic organisms containing a blue pigment in addition to chlorophyll; occur singly or in colonies in diverse habitats; important as phytoplankton.
Degree Heating Week (DHW)	indicates the accumulated thermal stress that coral reefs experience. A DHW is equivalent to one week of sea surface temperature 1°C above the expected summertime maximum. For example, 2 DHWs indicate one week of 2°C above the expected summertime maximum.
Depensatory	reduced survival or production of eggs or offspring because of a decrease in spawning stock.
Ecological epidemiology	A branch of epidemiology which views disease as a result of the ecological interactions between populations of hosts and parasites.
Ecoregion	an ecologically and geographically defined area smaller than a "realm" or "ecozone." Ecoregions cover relatively large areas of land or water, and contain characteristic, geographically distinct assemblages of natural communities and species. The biodiversity of flora, fauna and ecosystems that characterize an ecoregion tends to be distinct from that of other ecoregions.
Epibenthic	living on the surface of the ocean bottom.
Epizootic	an outbreak of disease affecting many animals of one kind at the same time.
ESA listing factors	(A) Present or threatened destruction, modification or curtailment of its habitat or range; (B) Overutilization for commercial, recreational, scientific or educational purposes; (C) Disease or predation; (D) Inadequacy of existing regulatory mechanisms; or (E) Other natural or manmade factors affecting its continued existence.
Etiology	the cause of a disease or abnormal condition.

Ex situ	outside of the original, natural, or existing place, position, or habitat (often referring to a zoo or laboratory).
Fleshy macroalgae	One of three functional groups of tropical reef algae; macroalgae are larger (canopy height usually >10mm), erect algae often with anatomically complex forms.
Fragmentation	Form of asexual reproduction in corals wherein a portion of a coral colony becomes physically separated, due to the breakage of the underlying coral skeleton, from the rest of the coral colony resulting in the production of live coral fragment clones. These fragment clones may reattach to the sea floor to grow into a new colony.
Gamete	A reproductive cell or sex cell that contains the haploid set of chromosomes, e.g. spermatozoon or sperm cell (male reproductive cell) and egg cell or ovum (female reproductive cell).
Genet	The sum of all ramets derived from a single zygote; synonym – genotype.
Genome sequencing	determining the order of DNA nucleotides, or bases, in a genome.
Genomics	a branch of Genetics used to define an organism in terms of the sequence of its genome.
Holobiont	a collective term referring to the totality of a coral animal, its endosymbiotic zooxanthellae, and the associated community of microorganisms.
In situ	in the natural or original position or place.
Land-Based Sources of Pollution (LBSP)	Pollution (including sediments and nutrients) from land-based sources such as development and construction activities, sewage treatment, agriculture, storm water, chemical and oil spills etc.
Lesion	any functional and morphological changes in coral tissue during disease (see Work and Aeby 2006).
Microsatellite	short sequences of di- or trinucleotide repeats of very variable length distributed widely throughout the genome.
Mono-specific thicket	a dense group of branching coral colonies composed of only one species.
Morbidity	a diseased condition or state.
Mucocyte	a mucus-secreting cell.
Nematocyte	a type of venomous cell unique to the phylum Cnidaria (corals, sea anemones, hydrae, jellyfish, etc.).

Nutrients	any substance assimilated by living things that promotes growth. The term is generally applied to nitrogen and phosphorus in wastewater, but is also applied to other essential and trace elements.
Phagocytic cell	a cell that ingests microorganisms and foreign particles.
Planulae	the very young, usually flattened oval or oblong free-swimming ciliated larva of a coral.
Ramet	An individual member of a cloned genotype.
Recruit	Coral larvae that have settled out of the water column and onto the sea floor that appear in the coral population and are detectable by human observers.
Resilience	is the rate at which a population returns to equilibrium after a disturbance takes it away from balance with its environment.
Resistant	the inherent ability of an organism to withstand harmful influences (as disease, toxic agents, or infection).
Robust Reference Populations	Populations of elkhorn or staghorn coral that exhibit high abundance and good coral colony condition.
Scleractinian	A coral with a hard calcareous skeleton, especially of the order Scleractinia.
Splice variant	a recombinant DNA molecule derived from cutting and resealing of DNA from different sources.
Tolerance	the ability of an organism to reproduce, grow, and survive within a range or gradient of particular environmental factors. These ranges are not fixed and can be dynamic over seasons or changing conditions.
Turf algae	densely packed algae, usually filamentous, which rise less than one centimeter above the substrate upon which they are growing.
Xenobiotic	a chemical compound (as a drug, pesticide, or carcinogen) that is foreign to a living organism.
Zooxanthellae	Symbiotic unicellular dinoflagellate algae, in the genus *Symbiodinium* that live in the tissues of many tropical animals such as corals, sea anemones, soft corals, tridacnid clams, some sponges and some foraminiferans.