Atlantic *Acropora* Status Review

March 3, 2005

Biological Review Team
Rafe Boulon, Mark Chiappone, Robert Halley, Walt Jaap, Brian Keller,
Bill Kruczynski, Margaret Miller, and Caroline Rogers

Acknowledgements

The status review for the Atlantic *Acropora* was conducted by a team of scientists from the National Marine Fisheries Service (NMFS), United States Geological Survey (USGS), the National Park Service (NPS) the states of Florida and North Carolina, the United States Environmental Protection Agency (USEPA) and the Florida Keys National Marine Sanctuary (FKNMS). The members of the biological review team (BRT) contributed a significant amount of time and effort to this process. The BRT included Mr. Rafe Boulon (NPS), Mr. Mark Chiappone (University of North Carolina-Wilmington), Dr. Robert Halley and Dr. Caroline Rogers (USGS), Mr. Walt Jaap (Fish and Wildlife Research Institute), Dr. Bill Kruczynski (USEPA), Dr. Brian Keller (FKNMS), and Dr. Margaret Miller (NMFS). Their review was dependent on information from scientific literature or data provided by various state agencies and individuals. For information provided to the BRT we particularly wish to acknowledge Dr. Andrew Bruckner, Dr. Richard Dodge, Dr. Dana Williams, Dr. Iliana Baums, Dr. Stephen Palumbi, Dr. Bernardo Vargas-Angel, Dr. Eugene Shinn, Mr. William Precht, Ms. Shannon Wade and Dr. Ron Hill. For assistance in coordinating and assisting the status review process in numerous ways, the BRT wishes to thank Ms. Mindy Hill, Ms. Maria Holliday and Ms. Fiona Wilmot. The BRT also appreciates the groundwork laid by the original Caribbean *Acropora* BRT during their short tenure. Members of that team included: Dr. Stephania Bolden, Dr. Andrew Bruckner, Mr. Richard Curry, Dr. Ronald Hill, Ms. Jennifer Jacukiewicz, Dr. Margaret Miller, Dr. Caroline Rogers, and Dr. Paul Sammarco. The BRT recognizes the efforts and coordination of the NMFS liaisons, Ms. Jennifer Moore and Dr. Stephania Bolden, for their assistance during this status review. Finally, the BRT wishes to thank Dr. Iliana Baums, Dr. Elizabeth Gladfelter, Dr. Judy Lang, Dr. Erich Mueller, Dr. Esther Peters, and Dr. Dana Williams, for their peer review of the status review.

This document should be cited as:

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

Cover Photo: Buck Island/Christiansted, Virgin Islands, 1966
Photo credit W. Williams, NPS

Table of Contents

List of Figures

List of Photos

List of Tables

List of Abbreviations

ADID	Advanced Identification of Disposal Areas
AGRRA	Atlantic and Gulf Rapid Reef Assessment
ATBA	Area To Be Avoided
BNP	Biscayne National Park
BRT	Biological Review Team
BIRNM	Buck Island Reef National Monument
BVI	British Virgin Islands
CBD	Center for Biological Diversity
CDHC	Coral Disease and Health Consortium
CITES	Convention on International Trade in Endangered Species
CRCCA	Coral Reef Conservation Act
CSA	Outer Continental Shelf Lands Act
CWA	Clean Water Act
CZMA	Coastal Zone Management Act
DNA	Deoxyribonucleic Acid
DNER	Department of Natural and Environmental Resources (Puerto Rico)
DTNP	Dry Tortugas National Park
EIS	Environmental Impact Statement
EEZ	Exclusive Economic Zone
EFH	Essential Fish Habitat
ERP	Environmental Resource Permit
ESA	Endangered Species Act
FDEP	Florida Department of Environmental Protection
FKNMS	Florida Keys National Marine Sanctuary
FKNMS(P)A	Florida Keys National Marine Sanctuary and Protection Act
FMC	Fishery Management Council
FMP	Fishery Management Plan
FR	Federal Register
FWI	French West Indies
FWRI	Fish and Wildlife Research Institute
GCC	Global Climate Change
GCRMN	Global Coral Reef Monitoring Network
GIS	Geographic Information System
GMFMC	Gulf of Mexico Fishery Management Council
GPA	Global Programme of Action for the Protection of the Marine Environment from Land Based Activities
GPS	Global Positioning System
HAPC	Habitat Area of Particular Concern
ICRAN	International Coral Reef Action Network
ICRI	International Coral Reef Initiative
ICRIN	International Coral Reef Information Network
IMDG	International Maritime Dangerous Goods Code
IOC	Intergovernmental Oceanographic Commission

IOCARIBE	Intergovernmental Oceanographic Commission for the Caribbean
IRF	Island Resources Foundation
IUCN	The World Conservation Union
MARPOL	International Convention for the Prevention of Pollution from Ships
MPA	Marine Protected Area
MSD	Marine Sanitation Device
NCRI	National Coral Reef Institute
NDZ	No Discharge Zone
NMFS	National Marine Fisheries Service
NMSA	National Marine Sanctuaries Act
NOAA	National Oceanic and Atmospheric Administration
NPDES	National Pollutant Discharge Elimination System program
NPS	National Park Service
NURC	NOAA's National Undersea Research Center
OCS	Outer Continental Shelf
OFW	Outstanding Florida Waters
PSSA	Particularly Sensitive Sea Areas
RHA	Rivers and Harbor Act
SAFMC	South Atlantic Fishery Management Council
SEFL	Southeast Florida
SHARQ	Submersible Habitat for Analyzing Reef Quality
SMMA	Soufriere Marine Management Area
SPAW	Specially Protected Areas and Wildlife
SPGP	State Programmatic General Permit
SR	Status Review
SST	Sea Surface Temperature
USCRTF	United States Coral Reef Task Force
UNEP	United Nations Environment Programme
UNESCO	United Nations Educational, Scientific and Cultural Organization
USEPA	United States Environmental Protection Agency
USFWS	United States Fish and Wildlife Service
USGS	United States Geological Survey
U.S.V.I.	United States Virgin Islands
UV	Ultraviolet
VICRNM	Virgin Islands Coral Reef National Monument
VINP	Virgin Island National Park
WBD	White Band Disease
WRP	Wetland Resource Permit
WPx	White Pox

Glossary of Terms
(as defined for use in this document)

Ahermatypic Non reef-building.

Anastomose The process wherein branches of a coral grow back together after the initial division.

Anthropogenic Of human origin.

Asexual reproduction Reproduction by fragmentation (segmentation or breakage) whereby all resulting colonies comprise a single genet.

Back reef The reef area landward of the reef crest.

Barrier reef An elongated reef parallel to the coastline and separated from it by a lagoon or channel of variable extent.

Benthic Bottom-dwelling; occurring on the sea floor.

Bioerosion Erosion produced by the action of organisms.

Biogenic Of biologic origin.

Bleaching The process whereby corals pale or whiten due to loss or decline of the pigments within symbiotic zooxanthellae or expulsion of the symbiotic algae from the coral tissue.

Brooding In corals, retention of developing larvae within the parent polyp until an advanced stage.

Calcareous Containing a significant amount of calcium carbonate ($CaCO_3$).

Calcification The process whereby corals grow by forming hard calcium carbonate skeletons.

Calice Oral surface of the corallite, often bowl shaped (concave).

Calicoblastic epithelial cells Epithelial cells that produce calcium carbonate crystals to build the corallite skeleton.

Carbon-14 dating A radiometric dating method based on the decay of the carbon-14 isotope (^{14}C) in carbon containing materials; useful for estimating age in the range of 200-40,000 years.

Caribbean Sea The geographic region considered in this status review wherein Atlantic *Acropora* spp. (*A. palmata*, *A. cervicornis*, and *A. prolifera*) are located. Defined as the area between latitudes 8 and 27^{o}N, and longitudes 59 to 97^{o}W, but also including a single point (Flower Garden Banks National Marine Sanctuary in the northern Gulf of Mexico) at 28^{o}N. Generally includes the following areas: southeast Florida and Florida Keys, the Bahamas, Cuba, Cayman Islands, Navassa, Jamaica, Hispaniola, Puerto Rico, Virgin Islands (both U.S. and British), Turks and Caicos, Greater and Lesser Antilles, Trinidad and Tobago, Grenada, Netherlands Antilles, Columbia, Venezuela, and the Caribbean coast of Central America including the countries of Panama, Costa Rica, Nicaragua, Honduras, Belize, Guatemala, and Mexico (southwest Gulf), and Flower Garden Banks (See Figure 3).

Clone Genetically identical group of individuals derived from a single individual by asexual reproduction.

Cnidarian Any of the members of the Phylum Cnidaria possessing nematocysts or stinging apparatus and exhibiting diploblasticity.

Columella The skeletal structure developed in the bottom-center of the corallite by the inner elements of the septa; often forms a spike or series of spines.

Community Assemblage of populations.

Competition The interaction among organisms for the same limited resource.

Coral reef Limestone structure built up through the constructional cementing and depositional activities of hermatypic fauna (e.g., stony corals) and flora (e.g., coralline algae).

Corallite The skeleton of an individual coral polyp.

Corallum The skeleton of a coral colony or solitary coral.

Dinoflagellate Single-celled algae having a flagellum during at least one stage of development.

Diploblastic Having two embryonic tissue layers: ectoderm and endoderm.

Epidermis Surface (outer tissue) layer of a coral polyp derived from the embryonic ectoderm.

Estuary A mixing zone of fresh water and seawater.

Etiology The study of the causes and origination of diseases – the cause(s) of a disease.

Extirpation Disappearance of an organism in a local area.

Extinction The total disappearance of an organism so that it no longer exists anywhere.

Extratentacular budding Formation of new coral polyps from outside the ring of tentacles of the parent polyp.
Eutrophic Defining a body of water with excessive nutrients.

Fecundity Ability of an organism to produce eggs or offspring; rate of production of offspring by a female.

Fusiform A spindle shape, tapering at the ends.

Fore reef The zone seaward of reef crest.

Fringing reef A coral reef that forms immediately adjacent to a land mass.

Endoderm The inner tissue layer of a coral polyp.

Gastrodermis The inner tissue layer of a coral polyp derived from the embryonic endoderm.

Genet Organism or group of organisms derived from a single zygote.

Genetic diversity Variation on the level of individual genes in a population that contributes to the ability of the organisms to evolve and adapt to new conditions

Genotype The genetic constitution of an organism, or a group of organisms sharing a specific genetic constitution. If all group members are identical by descent this group constitutes a clone.

Genotypic diversity The number of genetic individuals (genets) in a population.

Hermatypic Reef-building.

Heterozygosity The presence of different alleles at one or more loci on homologous chromosomes.

Holocene The most recent age of the Quaternary sub-era; the last 10,000 years.

Limestone A sedimentary rock consisting largely of calcium carbonate ($CaCO_3$).

Mesentery A vertical partition of tissue attached to the inner portion of the oral disc and the column wall of the polyp, partially attached to the action pharynx, providing structural support to the polyp between the septa.

Mesoglea Jelly-like layer that separates the ectodermic and the endodermic tissues of a coral polyp, derived from the ectoderm, and containing varying number of cells (ameobocytes, fibroblasts).

Monoclonal Consisting of a single genotype.

Nematocyst Stinging or adhesive organelle used in aggression, defense and food gathering by coral polyps.

Oligotrophic Defining a body of water with limiting levels of nutrients.

Origination The first appearance of an organism in the geologic record.

Overfishing Extraction of biomass beyond sustainable levels.

Patch reef A small, mound-like reef.

Planula Free-swimming larval stage of the Class Anthozoa, including scleractinian corals.

Polyps Individual unit of a colony that interconnects (see Figure 1).

Ramet Genetically identical but physiologically independent members of a genet.

Recovery To regain prior status or abundance.

Recruitment Addition of new individuals to a population.

Reef crest Shallowest portion of a reef tract that is sometimes emergent at low tide.

Septum Dividing the calcium carbonate wall of a corallite.

Sexual reproduction Reproduction by gametogenesis (development of gonads to produce eggs and sperm) and fertilization wherein a zygote is formed. The resulting individuals represent unique genotypes.

Septotheca Corallite wall formed by the outer portions of the septa.

Spur and groove A system of coralline ridges or fingers and sand grooves oriented perpendicular to the predominant swell.

Stony coral Colonial and solitary, hydrozoans and anthozoans of the Phylum Cnidaria depositing calcium carbonate exoskeletons.

Symbiotic Referring to or defining organisms that live in association with other kinds of organisms.

Synapticula Small bars of calcium carbonate that connect adjacent septa - they penetrate through the tissues (mesentery).

Tentacle Tubular extension of the polyp tissues originating in the area outside of the mouth; may be simple (single terminal end) or compound (multiple terminal ends).

Thicket A dense growth of branching corals, where individual colonies are not readily distinguishable.

Trabecula A pillar of calcareous fibers; multiple trabaculae joined together to build the skeletal mass of the septa and other corallite structures; the building block of the coral skeleton.

Triploblastic Having three embryonic tissue layers: endoderm, mesoderm and ectoderm.

Zooxanthellae Unicellular, dinoflagellate, symbiotic algae living within the endodermic tissues of many of the Milleporina, Octocorallia, Actinaria, Corallimorphia, Zooanthidea, and Scleractinia that provide a photosynthetic contribution to the coral's energy budget, enhance calcification, and give the coral much of its color.

1 Executive Summary

The National Marine Fisheries Service (NMFS) received a petition to list three Atlantic corals (*Acropora palmata*, *A. cervicornis* and *A. prolifera*) as either threatened or endangered under the Endangered Species Act (ESA). Following NMFS' positive 90-day finding, wherein the petition was determined to contain substantial information, an Atlantic *Acropora* Biological Review Team (BRT) was established to review the status of the corals concerned.

During deliberations, the BRT met to analyze and summarize the state of the corals to date. This document is the BRT's status review of the three *Acropora* spp., as guided by the ESA. It presents a summary of published literature and other currently available scientific information regarding the biology and status of the three corals, as well as an assessment of existing regulatory mechanisms and current conservation and research efforts that may yield protection. Notably, when species- or genera-specific information was not available for the Atlantic *Acropora* spp., the BRT considered threat information from knowledge about Caribbean reef corals and ecosystems.

Scleractinian corals present several particular challenges with regard to the evaluation of status under the ESA. First, as invertebrates, a listing determination must be based on the species' status throughout "all or a significant portion" of its range. Atlantic *Acropora* spp. are widely distributed, including the Caribbean, southeast Florida, and the Gulf of Mexico. *Acropora* spp. undergo both sexual (i.e., production of larvae) and, probably more commonly, asexual (i.e., fragmentation of branches can yield new attached and growing colonies) reproduction, so even a rigorous quantitative census of the abundance of colonies does not provide information on the number of genetic individuals. However, the density of genetic individuals determines in part if sexual reproduction, and thus recovery will be successful in this sedentary and self-incompatible group of corals.

Another difficulty involves the species status of *A. prolifera*. Although it has a history in the taxonomic literature, recent genetic research has determined that it is an F1 (i.e., first generation) hybrid between *A. cervicornis* and *A. palmata*. While there is genetic evidence that *A. prolifera* has backcrossed with *A. cervicornis* on evolutionary time scales, and it undergoes gametogenesis, as yet there is no evidence that it interbreeds with itself (i.e., produces sexual offspring in a cross between two *A. prolifera* colonies). For this reason, the BRT did not consider *A. prolifera* to meet the criteria for a species based on the ESA definition.

Acropora palmata and *A. cervicornis* used to be the most abundant and most important species on many Caribbean coral reefs in terms of accretion of reef structure. Both have high growth rates that have allowed reef growth to keep pace with past changes in sea level. Additionally, both exhibit branching morphologies that provide important habitat for other reef organisms; no other Caribbean reef-building coral species are able to fulfill these ecosystem functions. At the current reduced abundance of *A. palmata* and *A. cervicornis*, it is highly likely that both these ecosystem functions have been greatly compromised.

Both species underwent precipitous declines in the early 1980s throughout their ranges and this decline has continued. Although quantitative data on former distribution and abundance are scarce, in the few locations where quantitative data are available (e.g., Florida Keys, Dry Tortugas, Belize, Jamaica and the U.S.V.I.), declines in abundance (coverage and colony numbers) are estimated at >97%. Although this downward (decline) trend has been documented as continuing in the late 1990s, and even in the past five years in some locations, local extirpations (i.e., at the island or country scale) have not been rigorously documented. While recruitment of new colonies has been reported in various geographic locations, new recruits appear to be suffering mortality faster than they can mature (e.g., to sizes greater than 1 m in colony diameter). In a very few locations (e.g., Buck Island Reef National Monument) moderate recovery of *A. palmata* appears to be progressing. In most cases the origin of the recruits, presumably from sexual reproduction, is unknown so that their contribution to the corals' Caribbean-wide recovery remains undetermined.

In order to assess the five factors outlined in ESA section 4, the BRT categorized threats to *A. palmata* and *A. cervicornis* as *sources*, *stressors*, or *responses*. Sources were considered as natural or anthropogenic processes that create stressful conditions for organisms (e.g., climate change or coastal development). A stressor is the specific condition that causes stress to the organisms (e.g., elevated temperature or sediment runoff). The response of the organisms to that stressor is often in the form of altered physiological processes (e.g., bleaching, reduced fecundity or growth) or mortality. The BRT tabulated and then classified each stressor into one, or more, of the five ESA listing factors.

Disease, temperature-induced bleaching, and physical damage from hurricanes are deemed to be the greatest threats to *A. palmata* and *A. cervicornis*. The threat from disease, though clearly severe, is poorly understood in terms of etiology and possible links to anthropogenic stressors. Threats from anthropogenic physical damage (e.g., vessel groundings, anchors, divers/snorkelers), coastal development, competition and predation are deemed to be moderate. The threat from collection or harvest was deemed abated by effective national and international regulations.

The Atlantic *Acropora* BRT concludes that neither *A. palmata* nor *A. cervicornis* are in danger of extinction at the current time. However, both formerly super-abundant species have remained at extremely low levels of abundance for two decades without noticeable recovery and in most cases continued declines. The major threats to their persistence are severe, unpredictable, likely to increase in the foreseeable future (e.g., due to increases in global temperatures or coastal activities) and, at current levels of knowledge, unmanageable. In the meantime, managing some of the stressors ranked as less severe by the BRT (e.g., nutrients, sedimentation) may assist in decreasing the rate of *A. palmata* and *A. cervicornis* decline by enhancing coral condition and decreasing synergistic stress effects. For these reasons, the BRT concludes that *A. palmata* and *A. cervicornis* are not currently at risk of extinction but are likely to become so, within the foreseeable future.

2 General Introduction

NMFS received a petition from the Center for Biological Diversity (CBD) to list three Atlantic corals (*Acropora palmata*, *A. cervicornis* and *A. prolifera*) as either threatened or endangered under the Endangered Species Act (ESA). Following NMFS' positive 90-day finding, wherein the petition was determined to contain substantial information, the Southeast Regional Administrator of NMFS, who is charged with conducting the status review for the *Acropora* corals, convened an Atlantic *Acropora* Biological Review Team (BRT) to review the status of the corals concerned.

In order to conduct a comprehensive review, the BRT was asked by NMFS to assess the species' status and degree of threat to the species with regard to the factors for decline provided by section 4 of the ESA without making a listing determination. The BRT was provided a copy of the CBD petition and utilized the petition extensively during its consideration and analysis of potential threats to the corals. This status review document is a summary of the information assembled by the BRT and incorporates the best available scientific and commercial data available. In addition, the BRT summarized current conservation and research efforts that may yield protection, and drew scientific conclusions about the risk of extinction faced by each coral species under the assumption that the present conditions would continue (recognizing of course that natural demographic and environmental variability is an inherent feature of the "present" condition). The BRT is hopeful that the summary and analyses within this status review will assist NMFS in making its determination as to whether listing *Acropora* corals under the ESA is warranted.

2.1 The Endangered Species Act (ESA)

2.1.1 Candidate species / Species of Concern listing

As summarized in Bruckner (2002), NMFS began an analysis of the major reef-building coral species in 1998 to determine whether environmental or anthropogenic factors were threatening the survival of certain species in U.S. waters of the western Atlantic. Corals selected for this review were analyzed based on: (1) Their role in coral reef structure and function (e.g., reef growth, essential fish and invertebrate habitats, biodiversity and coastal protection) and (2) species potentially threatened by anthropogenic and natural factors identified as factors for decline under the ESA. This review included staghorn coral (*A. cervicornis*) and elkhorn coral (*A. palmata*) and seven other coral species previously identified in 1991 as "candidates" for listing under the ESA. All of those species were subsequently removed from the candidate list in 1997 because NMFS was not able to obtain sufficient information on their biological status and threats to meet the scientific documentation required for inclusion on the 1997 candidates list (62 FR 37560).

Utilizing data from the subsequent 1998 analysis, and information obtained during a public comment period, NMFS again added the two *Acropora* species, *A. palmata* and *A. cervicornis*, to the ESA candidate species list in 1999 (64 FR 33466). These two species qualified as ESA candidate species because there was some evidence they had undergone substantial declines in abundance or range from historic levels, and these declines were due to one or more of the five factors listed in the ESA (i.e., curtailment of habitat or range, overutilization, disease or predation, inadequacy of existing regulatory mechanisms, or other natural or manmade factors affecting their continued existence).

In 2004, NMFS established a "species of concern" list that essentially replaced the "candidate list" (69 FR 19976). Definitions provided in the notice for the two terms were as follows:

> *A "**candidate species**" refers to (1) species that are the subject of a petition to list and for which NMFS has determined that listing may be warranted pursuant to ESA section 4(b)(3)(A), and (2) species for which NMFS has determined, following a status review, that listing is warranted (whether or not they are the subject of a petition).*
>
> *A "**species of concern**" identifies species about which NMFS has some concerns regarding status and threats, but for which insufficient information is available to indicate a need to list the species under the ESA.*

NMFS believes that placing organisms on the species of concern list will achieve the following: (1) Identify species potentially at risk; (2) increase public awareness about the species; (3) identify data deficiencies and uncertainties in species' status and threats; (4) stimulate cooperative research efforts to obtain the information necessary to evaluate species status and threats; and (5) foster voluntary efforts to conserve the species before listing becomes warranted. NMFS hopes that these effects may reduce the future need to list such species as threatened or endangered under the ESA.

Following the NOAA 2004 policy, both *A. palmata* and *A. cervicornis* were transferred from the candidate species list to the species of concern list, but subsequently returned to candidate status when the positive 90-day finding, in response to the CBD petition, was published in June 2004. Notably, the designation of "candidate species" or "species of concern" does not confer any procedural or substantive protections of the ESA on the species (69 FR 19976).

2.1.2 ESA Background

The purposes of the ESA are to provide a means to conserve ecosystems upon which endangered species and threatened species depend, to provide a program for the conservation of endangered and threatened species, and to take appropriate steps to recover a species. The U.S. Fish and Wildlife Service (USFWS) and NMFS share responsibility for administering the ESA; NMFS is responsible for determining whether marine, estuarine or anadromous species, subspecies, or distinct population segments are threatened or endangered under the ESA. To be considered for listing under the ESA, a group of organisms must constitute a "species."

The ESA provides the following definitions:

> *"the term* ***species*** *includes any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature."*
>
> *"****endangered species****" is defined as "any species which is in danger of extinction throughout all or a significant portion of its range."*
>
> "***threatened species****" is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range."*

Additional criteria regarding entities appropriate for listing under the ESA have been set forth. First, there is the ability to identify and list distinct populations segments (61 FR 4722) or evolutionarily significant units (56 FR 58612) when a population satisfies the criteria of being discrete and significant; however these policies are limited to vertebrates and are therefore not within the scope of this *Acropora* status review (SR). Second, a draft policy for listing "hybrids" was proposed by NMFS and the USFWS in 1996 (61 FR 4710). The intent of the draft policy (which was never finalized and is therefore non-binding) was to include intercrossed individuals within the original listing action for the parent entity (thereby affording ESA protections) if the individual was more similar to the listed parent. Introgression (the transfer of genetic material from one taxonomic species to another, and its spread among individuals of the second species) is found throughout the plant and animal kingdoms. Given the low densities of many populations of threatened and endangered species, such introgression may be experienced by some listed species as a result of the decline of conspecific mates. The draft policy specifically addresses intercrossed progeny produced as a result of a cross between an individual of a listed taxon and an individual of a taxon that is not listed. The protections of the ESA would extend to those intercross progeny if: (1) the progeny share the traits that characterize the taxon of the listed parent, and (2) the progeny more closely resemble the listed parent's taxon than an entity intermediate between it and the other known or suspected non-listed parental stock. Finally, in order for a species believed to be of hybrid origin to maintain eligibility for listing, it must: (1) be developed outside of confinement, (2) be a self-sustaining, naturally occurring taxonomic species, and (3) meet the criteria for threatened or endangered species under the ESA.

The process for determining whether a species (as defined above) should be listed is based upon the best available scientific and commercial information. The status is determined from an assessment of factors specified in section 4 (a)(1) of the ESA that may be contributing to decline, including:

(A) The 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 the continued existence of the species.

Within this SR, the BRT also summarized ongoing protective efforts to determine if they abate any risks to the corals.

When a species is listed as endangered under the ESA, it is afforded all protections of the ESA, including the development and implementation of recovery plans, requirements that Federal agencies use their authorities to conserve the species, and prohibitions against certain practices, such as taking individuals of the species. Under NMFS policy, when a species is listed as threatened, the prohibitions for take are not automatically afforded. These prohibitions must be specifically afforded to a threatened species through a special rule (section 4(d) of ESA). Specifically, the prohibitions of section 9 of the ESA, in part, make it illegal for any person subject to the jurisdiction of the United States: to take (i.e., to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture or collect, or to attempt to engage in any such conduct); to import into, or export from, the United States; to ship in interstate or foreign commerce in the course of commercial activity; or to sell or offer for sale in interstate or foreign commerce any endangered wildlife. To possess, sell, deliver, carry, transport, or ship, endangered wildlife that has been taken illegally is also prohibited. However, section 10 of the ESA provides NMFS with the authority to grant exemptions to the section 9 taking prohibitions for scientific research, enhancement, and incidental take permits. The ESA provides some exceptions to the prohibitions, without permits, for certain antique articles and species held in captivity at the time of the listing. The ESA also provides for possible land acquisitions and cooperation with the states.

In some instances, species that are not listed under the ESA are afforded protection. For example Section 4(e) of the ESA, entitled “Similarity of Appearance Cases,” allows the Secretary (of Commerce or Interior), by regulation of commerce or taking, to the extent he deems advisable, to treat any species as an endangered species or threatened species even though it is not listed if he finds that: (1) Such species so closely resembles a listed species in appearance, that enforcement personnel would have substantial difficulty in differentiating between the listed and unlisted species; (2) the effect of this substantial difficulty is an additional threat to an endangered or threatened species; and (3) such treatment of an unlisted species will substantially facilitate the enforcement and further the policy of the ESA.

2.1.3 The petition

On March 4, 2004, CBD petitioned NMFS under the ESA, requesting that elkhorn coral (*Acropora palmata*), staghorn coral (*A. cervicornis*), and fused-staghorn (*A. prolifera*) coral be listed as endangered or threatened species, and critical habitat be designated. On June 23, 2004, NMFS made a positive finding (69 FR 34995) that CBD presented substantial information indicating the action may be warranted. NMFS convened this BRT, comprised of experts in the field, to develop this SR of the three corals. Pursuant to NOAA’s 2004 policy defining species of concern and candidate species, once a positive

90-day finding has been issued, a species of concern is identified as a "candidate species." Therefore, the three Atlantic *Acropora* spp. are currently considered candidates under the ESA.

2.2 Corals and Reefs

Stony corals, like Atlantic *Acropora* spp., (Class Anthozoa, Order Scleractinia) are marine invertebrates that secrete a calcium carbonate skeleton. Stony corals include members of both the Class Hydrozoa (fire corals) and true stony corals (O. Scleractinia). The scleractinians can be hermatypic (significant contributors to the reef-building process) or ahermatypic, and may or may not contain endosymbiotic algae (zooxanthellae) (Schumacher and Zibrowius 1985). The largest colonial members of the Scleractinia help produce the carbonate structures known as coral reefs in shallow tropical and subtropical seas around the world. The rapid calcification rates of these organisms have been linked to the mutualistic association with single-celled dinoflagellate algae, zooxanthellae, found in the gastrodermal cells of the coral tissues (Goreau et al. 1979). Massive and branching stony corals are the major framework builders and a source of carbonate sediment on the reef. Corals provide substrate for colonization by benthic organisms, construct complex protective habitats for a myriad of other species including commercially important invertebrates and fishes, and serve as food resources for a variety of animals.

Atlantic *Acropora* spp. are found on shallow tropical reefs throughout the wider Caribbean, including the southwestern Gulf of Mexico, Caribbean coasts of Central and South America, the Bahamian archipelago, and the Greater and Lesser Antilles. For the purposes of this report, shallow tropical reefs are defined as those occurring in subtropical and tropical areas in water depths less than 30 m, within the upper photic zone. *Acropora* spp., like other zooxanthellate corals, host symbiotic dinoflagellates from the Genus *Symbiodinium*, which provide a phototrophic contribution to the coral's energy budget, enhance calcification, and give the coral most of its color.

The scleractinian corals, along with dinosaurs and mammals, evolved in the Middle of the Triassic Era (208 to 250 million years before present). Scleractinia are in the Class Anthozoa of the Phylum Cnidaria (Coelenterata), possessing radial symmetry. Cnidaria is one of two phyla that exhibit diploblastic (i.e., two tissue layers) tissue organization; all higher taxa are triploblastic (three-tissue layers) and thus contain a true mesoderm. The phylum is named Cnidaria because organisms use cnidae or nematocysts (capsules containing toxin and hollow inverted tubule that, when triggered, evert and pierce prey or predator, injecting the toxin) for prey capture and self-defense. Organisms in the phylum can be solitary (one polyp) or colonial (many polyps).

The Scleractinia have diversified into multiple families, all of which exploit the ability to form complex colonies consisting of many individual polyps. The individual building unit in a colony is termed a polyp: a sac with mouth and tentacles on the upper side (Figure 1).

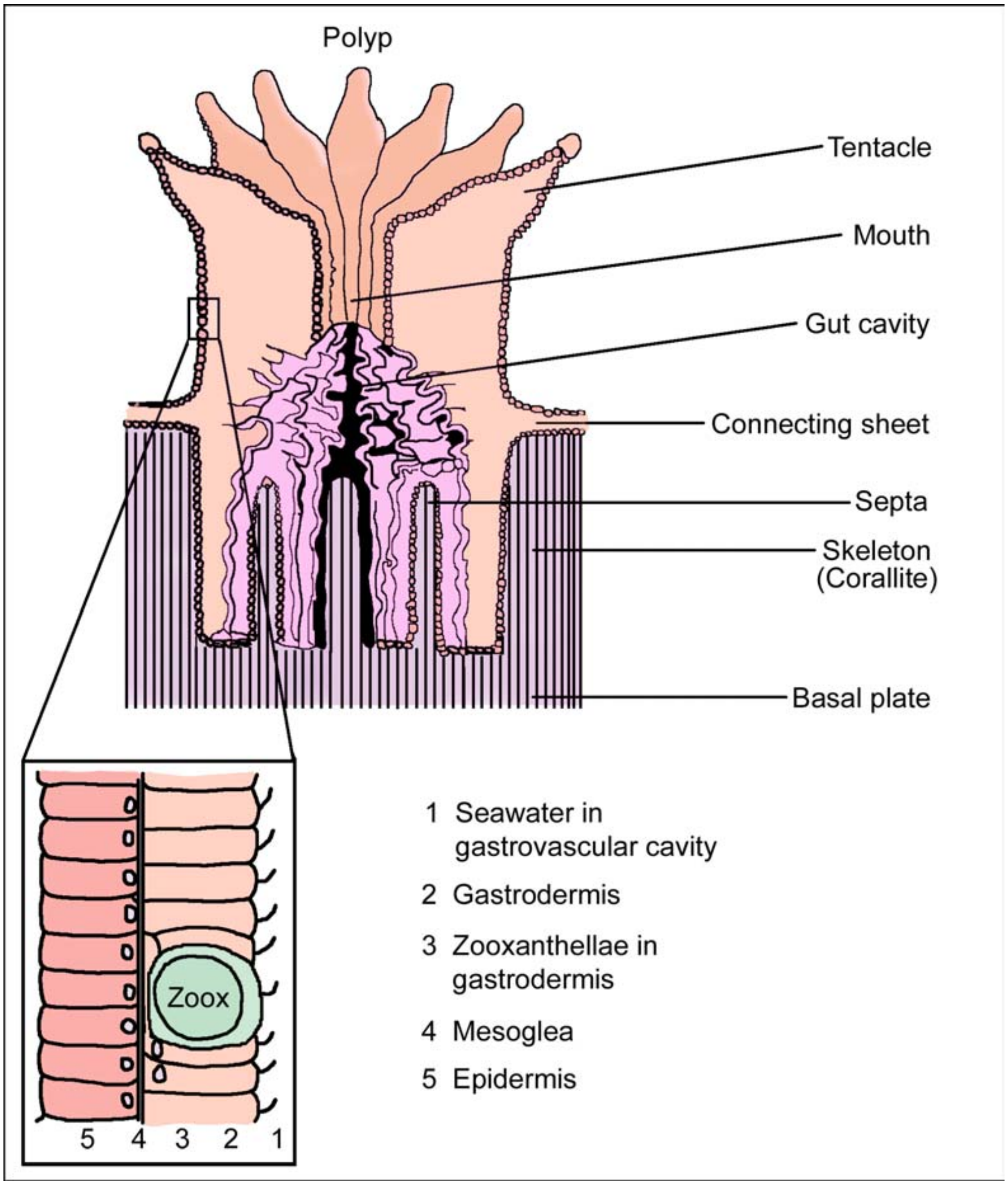


Figure 1. Schematic of coral polyp (corallite) anatomy (Adapted from Sumich 1996).

General coral reproduction

Life for a coral begins with a sperm fertilizing an egg. Embryonic development results in a planula larva. The larvae are free living in the plankton and may survive long periods (i.e., weeks) floating in the water currents. Upon maturing, larvae seek a place to settle on the sea floor. There is some evidence that chemical signals from crustose coralline algae or other corals of the same species stimulate settlement (Morse et al. 1994, Morse and Morse 1996). Settled larvae undergo metamorphosis by generating a calcium carbonate, tubular skeleton. The mouth is situated at the upper end and a ring of tentacles develops around the mouth. After the initial transformation into a polyp unit, expansion occurs with new polyps budding from the original one. Each bud develops into a functioning polyp with connecting skeleton (Photo 1). The colony expands outward in multiple dimensions; in massive corals the typical morphology is hemispherical. In branching corals like *Acropora,* branches sprout from an initial stem forming a bush-like structure. Each polyp is an individual: it captures its own food, and has its own digestive, nervous, respiratory, and reproductive systems. A large coral colony has thousands of corallite/polyps working semi-independently to sustain the colony. In some species it appears that there is virtually no limit to colony size, as polyps can bud indefinitely.

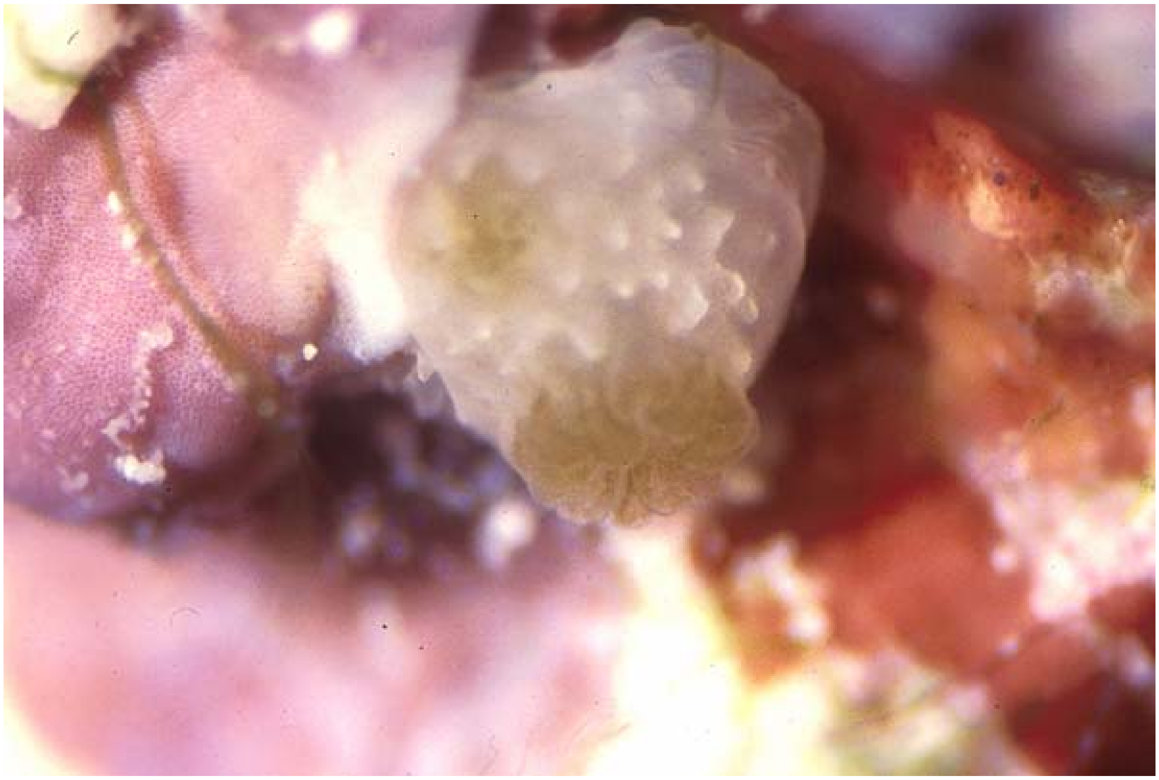


Photo 1. Initial polyp with developed skeleton and first budding polyp on the side. Photo credit A. Szmant.

Clonal life history

Acroporid corals are clonal, colonial invertebrates, which make them unique among species that have been considered for ESA listing. Most zooxanthellate corals (including *Acropora* spp.) are colonial and grow by the addition of new units called polyps. By the same token, colonies can exhibit partial mortality whereby a subset of the polyps in a colony die, but the remainder of the colony persists. Colonial species present a special challenge in determining the appropriate unit to evaluate for status (i.e., abundance).

In addition, because *Acropora* spp. are clonal, new colonies can be added to a population by fragmentation (breakage from an existing colony of a branch that re-attaches to the substrate and grows) as well as by sexual reproduction (see Section 4.2). Fragmentation results in multiple colonies (ramets) that are genetically identical, while sexual reproduction results in the creation of new genotypes (genets). Thus, in corals, the term "individual" can be interpreted as the polyp, the colony, or the genet (Hughes et al. 1992).

In clonal species, such as *Acropora* spp., there are several levels of genetic variability to be considered. Because a coral colony can proliferate by fragmentation, there may be many colonies on a reef, but only one or a few genotypes; that is, most or all of the colonies may have originated from fragments (i.e., are clones) of a single colony. In this instance, they are ramets and share the same genotype, as do identical twins. The first level of analysis of any population genetic study of *Acropora* spp. would be to determine how many genotypes are represented by the individual colonies found, whether on a given reef or throughout its range. This is termed the "genotypic diversity" and simply indicates the number of genetic individuals. Genotypic diversity is influenced by the relative contribution of sexual versus asexual reproduction in a population. Because fragmentation (asexual) and sexual reproduction occur in clonal species (such as *Acropora* spp.) to varying degrees within the same populations, genotypic diversity can vary widely, even at small spatial scales (e.g., hundreds of meters). Single clones may dominate or exclusively occupy areas of tens to hundreds of square meters. At the other extreme, virtually every colony at this scale might consist of genetically distinct individuals that recruited via sexual reproduction. If there is low genotypic diversity within individual stands and/or across the region, it might suggest that a clonal species' status is under much greater threat than would be judged from its overall abundance because the effective population size would be much smaller than the colony abundance would suggest. Consequences of high clonality include poor to no reproductive output (since Atlantic *Acropora* spp. do not self-fertilize) and potential increased susceptibility to stress events for which that clone is not adapted.

The next level of analysis concerns the amount of "genetic diversity," or the amount of variability among genetic individuals (or 'genets'). Genetic diversity is directly comparable to what would be commonly measured in a vertebrate, for example, and describes the number of variants ("alleles") of each gene that are present in the population and how these variants are distributed among individuals (often expressed as the "heterozygosity" of individuals and populations). Genetic diversity is influenced by processes such as genetic drift, inbreeding, and selection. While both levels of genetic variability are important to consider when assessing extinction risk, of the two, genetic diversity is the more difficult to measure.

Reef Zonation

Coral reefs are shallow-water, tropical-subtropical systems characterized by a great diversity of plants and animals associated with the reef structure, as well as by high rates of primary production in relatively nutrient-poor waters (Lewis 1981). Fagerstrom (1987) listed several definitive characteristics of reefs, including those constructed by Atlantic reef-building *Acropora* spp.:

- A rigid framework is present;
- The skeletons or other calcareous micro-structures are abundant;
- Structures have positive topographic relief;
- Framework organisms have rapid growth rates; and
- Taxonomic diversity is high, with several ecological functional groups.

Some coral reefs exhibit zonation based on bathymetry and associations of organisms (Figure 2). In the decades of the 1960s and 1970s, many Caribbean reefs were described as having an elkhorn (*A. palmata*) zone and a staghorn (*A. cervicornis*) zone, based upon high coverage and colony density, and in some cases near exclusiveness, of these species at particular depths. Typically, the elkhorn zone extended from the surface to about 5 m depth and the staghorn zone from about 7 to 15 m depth. These zones no longer exist in their historic configurations, due to their diminished abundances on Caribbean reefs, and in many locations now consist of algae colonizing dead *Acropora* framework.

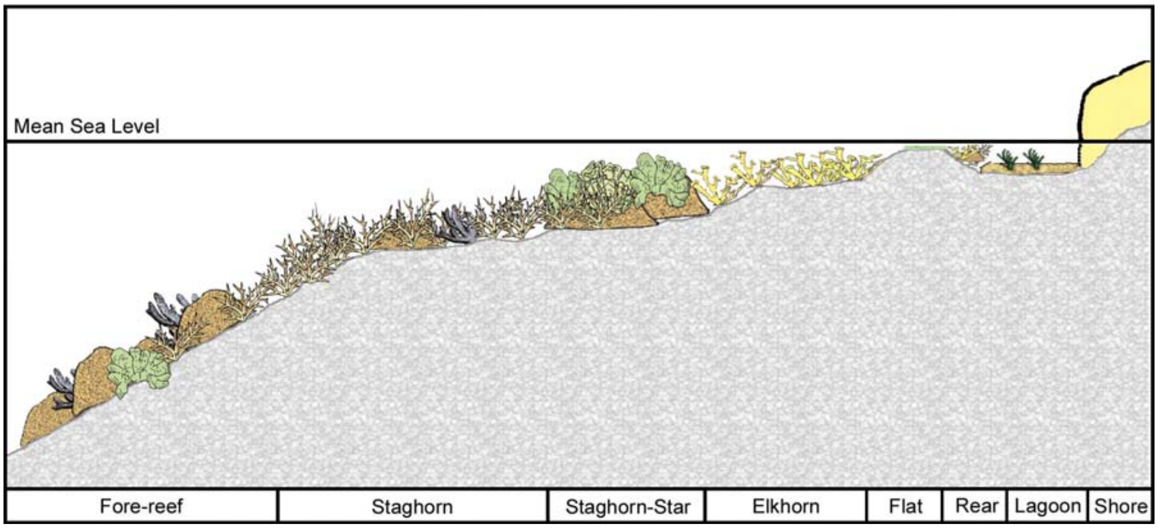


Figure 2. Reef zonation schematic example modified from several reef zonation-descriptive studies (Goreau 1959; Kinzie 1973; Bak 1977).

Since the early 1980s, a series of dramatic events precipitated drastic departures from the historic zonation pattern on most Caribbean reefs. These disturbances included a series of severe hurricanes, the Caribbean-wide die-off of the important herbivorous sea urchin, *Diadema antillarum*, and the widespread mortality of *A. palmata* and *A. cervicornis* due to disease, resulting in an overall decline in coral cover coinciding with a dramatic increase in the cover of macroalgae (seaweeds). Aronson and Precht (2001) argued that the *Acropora* spp. die-off was the primary cause of this shift in benthic community structure, while Hughes (1994) and other authors have maintained that changes in the herbivory regime (overfishing and *Diadema* die-off) are primarily responsible. It is clear that this shift was the result of multiple disturbances and that many of their effects have not been abated on a Caribbean-wide scale. That is, *Diadema antillarum*, *A. palmata*, and *A. cervicornis* have not shown substantial recovery, and heavy fishing pressure restricts herbivorous fish abundances to low levels on several Caribbean reefs. Simultaneously, macroalgae still dominate many Caribbean coral-reef substrates. Hence, the classic reef zonation patterns described above do not reflect Caribbean reef structure today, and it is possible that the present pattern will persist for the foreseeable future.

3 Taxonomy and Species 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). *Acropora* is the only member of the family currently found in the western Atlantic; the other genera are restricted to the Pacific and Indian Oceans, including the Red Sea.

Family Diagnosis
Genera in the family Acroporidae form branching and massive colonies by extratentacular budding (Vaughn and Wells 1943). Corallites are relatively small, with porous walls constructed by synapticula that merge with the non-corallite skeleton. The septa do not extend above the corallite and are in two cycles, constructed by trabeculae. Columella are usually not present, and the skeletal material between the corallites is flake-like, spiny, or striated.

Genus *Acropora* Oken 1915

Etymology: The literal translation of *Acropora* is: a porous stem or branch.

Type species is *Millepora muricata* Linnaeus 1758, designated by the International Commission on Zoological Nomenclature in 1963.

Genus Diagnosis
Colonies of *Acropora* exhibit mostly branching, encrusting, rarely submassive colonial morphologies. Species of *Acropora* exhibit an extremely wide breadth of growth forms (e.g., staghorns, bushes, plates, tables, columns). Branches have an axial terminal corallite, with radial corallites surrounding the axial corallite. All species contain zooxanthellae in their soft tissue. *Acropora* has 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.

In the 19th century, virtually all *Acropora* spp. were included in the genus *Madrepora*. Classic taxonomic publications of this era include Lamarck (1816), Ehrenberg (1834), Dana (1846), and Brook (1893). In 1902, Verrill established usage of *Acropora* for the genus. In their reversionary work Veron and Wallace (1984) studied approximately 4,500 specimens of *Acropora* from eastern Australia and recognized 73 species. Presently 368 nominal *Acropora* species (world-wide) are known from the literature (Veron 1986); of these only three (two species and one hybrid) occur in the western Atlantic.

SPECIES ACCOUNTS

Acropora cervicornis (Lamarck, 1816)

Madrepora cervicornis Lamarck, 1816
Acropora cervicornis (Lamarck) Verrill, 1902
Acropora cervicornis (Lamarck) Almy and Carrión-Torres, 1963
Acropora cervicornis (Lamarck) Roos, 1971
Acropora cervicornis (Lamarck) Wells and Lang, 1973
Acropora cervicornis (Lamarck) Bak, 1975
Acropora cervicornis (Lamarck) Shinn, 1976
Acropora cervicornis (Lamarck) Cairns, 1982
Acropora cervicornis (Lamarck) Jaap, 1984
Acropora cervicornis (Lamarck) Veron, 2000
Acropora cervicornis (Lamarck) Cairns et al., 2002

Etymology: The literal translation of *cervicornis* is: related to a deer antler.

Common name: The common name of *A. cervicornis* is staghorn coral.

Species Diagnosis

Characterized by staghorn-antler-like colonies, with cylindrical, straight or slightly curved branches. Prominent axial corallite at the branch tip; bract-like radial corallites symmetrically arranged around the branch, oriented toward the branch tip, converging at the axial corallite. Branching is irregular and secondary branches form at approximately 60 to 90 degrees relative to a primary branch. Individual colonies are up to 1.5 m across and typically form monospecific thickets. In calm-water conditions, the colonies have an open appearance with long stems between the diverging branches. In turbulent wave surge or currents the colonies are smaller with greater branch density. Branches of *A. cervicornis* rarely anastomose (grow back together) with adjoining branches. The diameter of the branches ranges from 0.25 to 1.5 cm. Tissue color ranges from golden-yellow to medium brown; growing tips tend to be lighter or lack color. Polyps are cream-white to light brown; tentacles with blunt tips extend a short distance above the calice. The colony may or may not be firmly attached to the sea floor. During the 1970s there were vast fields (thickets) of *A. cervicornis* on many reefs, typically in fore- and back-reef areas, such fields of *A. cervicornis* are rare today. The nominal situation in 2004 is isolated branches and small thickets, 0.5 to 1 meter across. Photos 2 to 5 exhibit colonies of *A. cervicornis*.

Photo 2. ***Acropora cervicornis*** **(Lamarck, 1816) Western Sambo Reef, Florida, note the origin of a new branch in the lower left. Photo credit W. Jaap.**

Photo 3. ***Acropora cervicornis*** **(Lamarck, 1816) Western Sambo Reef, Florida Keys. Specimen with open branching. Photo credit W. Jaap.**

Photo 4. ***Acropora cervicornis*** **(Lamarck, 1816) Western Sambo Reef, Florida, example of dense branching. Photo credit W. Jaap.**

Photo 5. ***Acropora cervicornis*** **(Lamarck, 1816) White Shoal, Dry Tortugas. Note white, exposed skeleton caused by predator or disease. Photo credit W. Jaap.**

Acropora palmata (Lamarck, 1816)

Madrepora palmata Lamarck, 1816
Madrepora muricata Duerdan, 1902
Madrepora (*Acropora*) *palmata* Mayer, 1914
Acropora palmata (Lamarck) Vaughan, 1915
Acropora palmata (Lamarck) Almy and Carrión-Torres, 1963
Acropora palmata (Lamarck) Roos, 1971
Acropora palmata (Lamarck) Wells and Lang, 1973
Acropora palmata (Lamarck) Bak, 1975
Acropora palmata (Lamarck) Cairns, 1982
Acropora palmata (Lamarck) Jaap, 1984
Acropora palmata (Lamarck) Veron, 2000
Acropora palmata (Lamarck) Cairns et al., 2002

Etymology: The literal translation of *palmata* is: related to a palm branch.

Common name: The common name of *A. palmata* is elkhorn coral.

Species Diagnosis

Largest of all species of *Acropora* (Veron 2000) and considered a Caribbean reef icon. Large specimens are at least two meters high and four meters in diameter. Colonies are flattened to near round with frond-like branches. Branches typically radiate outward from a central trunk that is firmly attached to the sea floor. Corallites are tube-like and porous, 2 to 4 mm long, about 2 mm in diameter, white near the growing tip, and brown to tan away from the growing area. The axial and radial corallites are usually not distinctly different. The skeletal area between the corallites is rough-irregular and the tube-like corallites project upward. Colonies begin from a settled larvae or a fragment; settled larvae are undifferentiated and lack branching. As they grow, protuberances develop to generate the main column and radial branches. Polyps are creamy-white and inconspicuous tentacles protrude from the corallites. Photos 6 to 9 exhibit colonies of *A. palmata*.

Photo 6. ***Acropora palmata*** **(Lamarck, 1816) Western Sambo Reef, Florida. Note the new growth (white corallite projections) on the branch tips and the irregular growth on the base. Photo credit W. Jaap.**

.

Photo 7. ***Acropora palmata*** **(Lamarck, 1816) Garden Key, Dry Tortugas. Photo credit W. Jaap.**

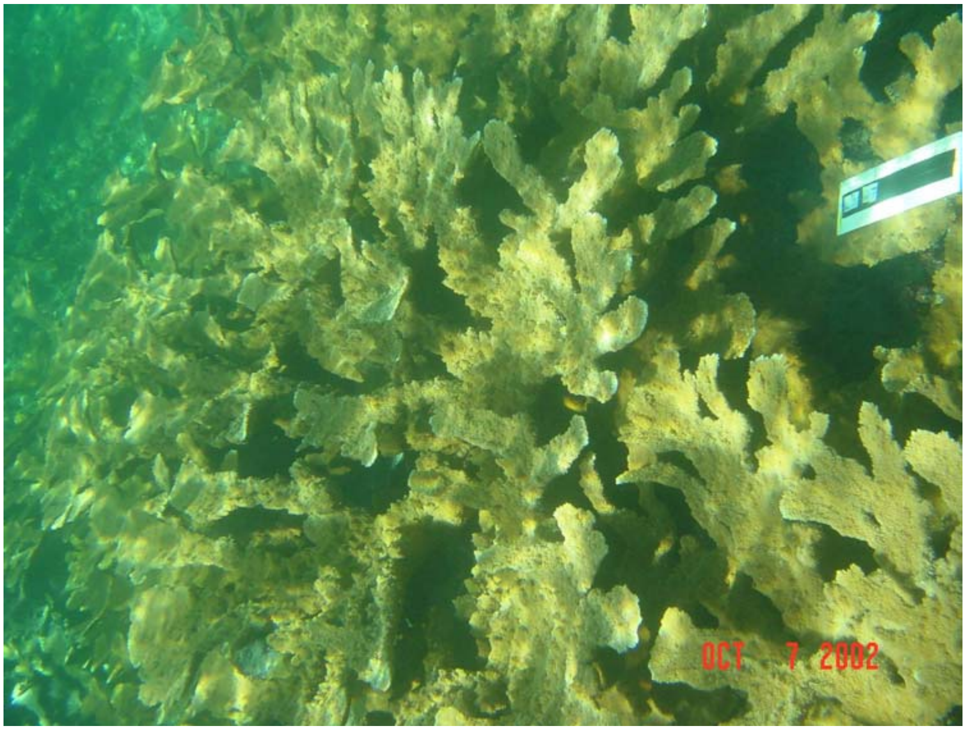


Photo 8. A thicket of *Acropora palmata* in the Exumas region of the Bahamas, 2002. Photo credit I. Baums.

Photo 9. *Acropora palmata* (Lamarck, 1816) Western Sambo Reef, Florida. Note the smaller under story colonies, presumably generated from upper story fragments. Photo credit W. Jaap.

Acropora prolifera (Lamarck, 1816)

Madrepora prolifera Lamarck, 1816
Acropora prolifera (Lamarck) Almy and Carrión-Torres, 1963
Acropora prolifera (Lamarck) Roos, 1971
Acropora prolifera (Lamarck) Bak, 1975
Acropora prolifera (Lamarck) Cairns, 1982
Acropora prolifera (Lamarck) Jaap, 1984
Acropora prolifera (Lamarck) Veron, 2000
Acropora prolifera (Lamarck) Cairns et al., 2002

Etymology: The literal translation of prolifera is: related to forming buds or branches.

Common name: The common name of *A. prolifera* is fused-staghorn coral.

Diagnosis

Acropora prolifera is also staghorn-like, with multiple branches that may fuse together or anastomose. The branches are very similar in diameter and corallite configuration to *A. cervicornis*, but there is also a palmate form. The branching froms a primary stem tends to be at angles that are 45 degrees or less. There is often a proliferation of branches at the end of principal stems exhibiting a fan-like appearance; these frequently fuse or anastomose. Axial corallites are approximately twice the diameter of the radial corallites. Colony color ranges from light yellow-gold to medium brown; branch tips tend to be lighter or lack color. Polyps are creamy-white to light brown with short tentacles. The colony may or may not be attached to the sea floor. Photos 10 to 13 exhibit *A. prolifera* colonies.

Species Status

Acropora prolifera is recognized in the taxonomic literature as a valid morphological species. It has always been rare, and little specific scientific information is available regarding its distribution, abundance, trends, or threats. There are, in fact, a wide range of intermediate morphologies that exist in nature (Photos 14a-f) and this further complicates the field assessment of abundance in *A. prolifera*. Recent scientific literature, however, indicates that individuals of *A. prolifera* sampled from throughout the Caribbean region were all F1 (i.e., first generation) hybrids of *A. palmata* and *A. cervicornis* (van Oppen et al. 2000, Vollmer and Palumbi 2002). This finding is consistent with the observed rarity of *A. prolifera*. There is also genetic evidence that *A. prolifera* has undergone rare backcrossing with the parent *A. cervicornis* on an evolutionary time scale (Vollmer and Palumbi 2002). It appears that *A. prolifera* does undergo gametogenesis, but there is no direct evidence that it is capable of forming successful sexual offspring. It is known that other Atlantic *Acropora* spp., though hermaphroditic, are not able to self-fertilize because eggs and sperm from genetically distinct colonies must mix to produce viable larvae. While it is unclear whether or not *A. prolifera's* gametes are viable, it is highly unlikely that genetically distinct colonies occur within sufficient proximity to routinely accomplish successful fertilization in nature. For these reasons the BRT considers *A. prolifera* a hybrid for the purposes of this status review as it is not known to interbreed, and therefore it does not meet the ESA definition of a species.

Photo 10. ***Acropora prolifera*** **(Lamarck, 1816) Garden Key, Dry Tortugas, Florida. Photo credit W. Jaap.**

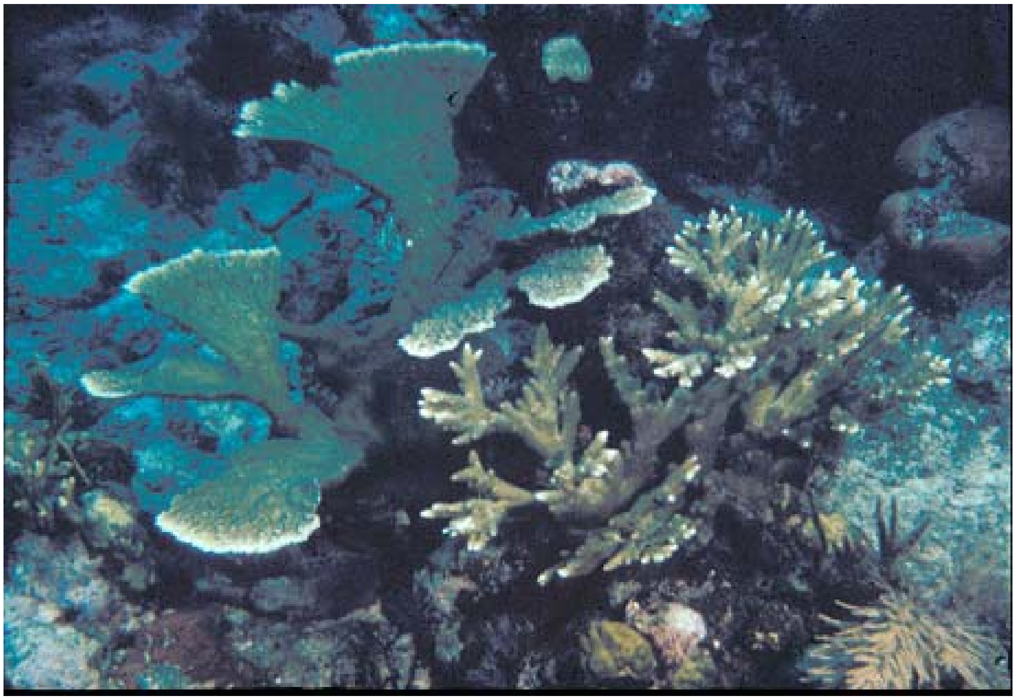


Photo 11. ***Acropora palmata (left) and A. prolifera*** **(right) Garden Key, Dry Tortugas. Photo credit W. Jaap.**

Photo 12. ***Acropora prolifera*** **(Lamarck, 1816) Garden Key, Dry Tortugas. Photo credit W. Jaap.**

Photo 13. ***Acropora prolifera*** **(Lamarck, 1816) Garden Key, Dry Tortugas. Photo credit W. Jaap.**

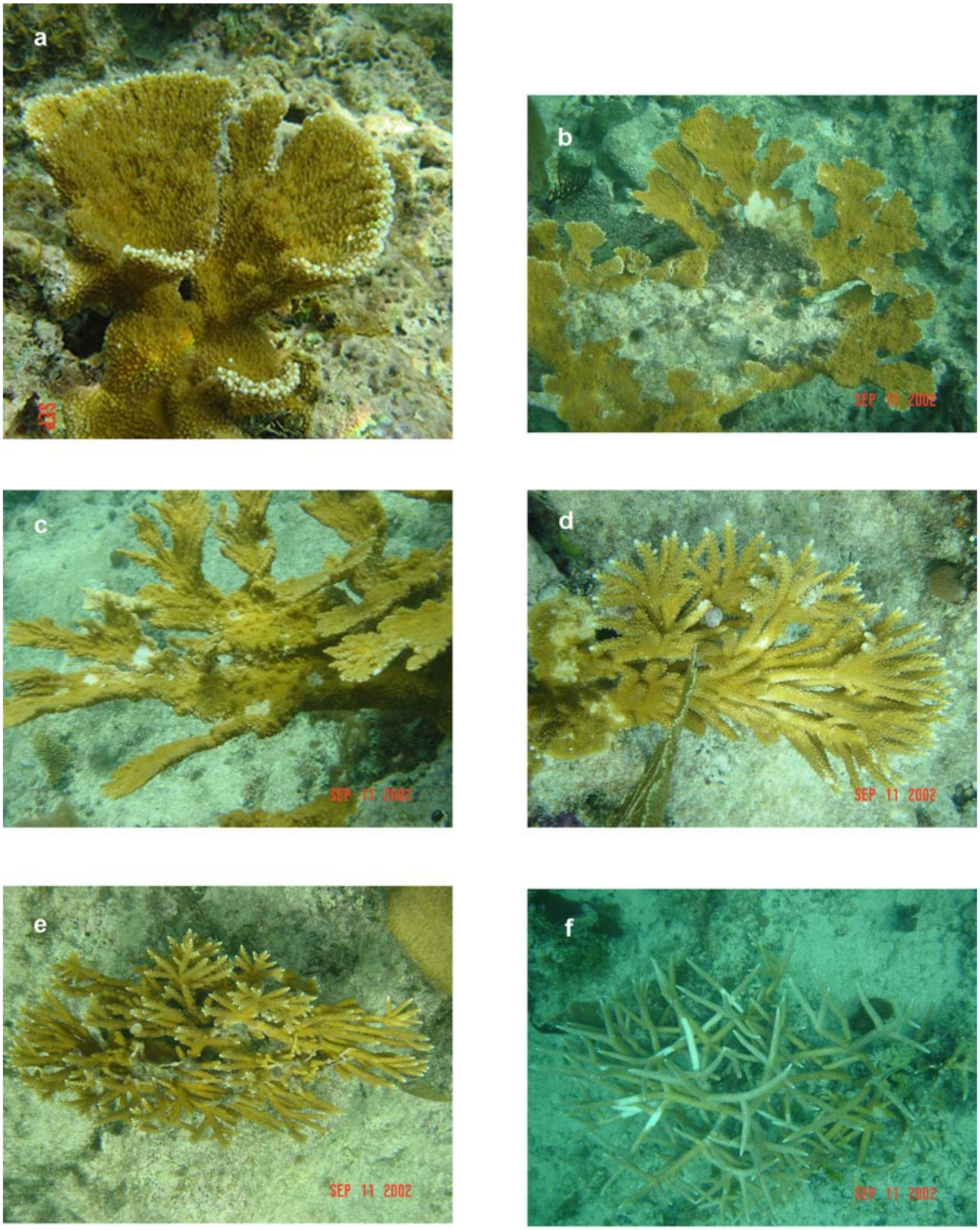


Photo 14. Variations in *Acropora. prolifera* morphology, ranging from *A. palmata*-like (a) to *A. cervicornis*-like (f). The colony morphologies shown here all co-occurred at the same site, Hull Bay, St. Thomas, U.S.V.I. Photo credit M. Miller.

4 Natural History

The following is a brief comprehensive sketch of the biological characteristics, environmental requirements, and ecosystem function of *A. palmata*, *A. cervicornis*, and when available, *A. prolifera*. Status and trends of the abundance and distribution across their geographic range are presented, along with a few case studies detailing specific quantitative data. Following the assessment of current patterns of abundance is a summary of the two species in the geologic record. Because of their calcium carbonate skeleton, they are persistent in the geologic record, allowing for carbon-14 dating and stratigraphic analysis. Finally, current atmospheric conditions are summarized and their impacts to corals, specifically to *Acropora* spp. when possible, are summarized.

4.1 Morphology, Growth, Habitat, and Environmental Requirements

This section describes morphological variability, growth, growth rate, and habitat requirements of *A. cervicornis* and *A. palmata*. Environmental influences result in various morphological adaptations in both coral species; for example, colonies in areas with strong wave action or currents are often compact with blunt and short branches. Water depth influences light attenuation, wave energy, and sedimentation, all of which can influence the life history processes of these corals.

Acropora cervicornis

Historically, *A. cervicornis* was reported from depths ranging from <1 to 60 m (Goreau and Goreau 1973). We suspect that 60 m is an extreme situation and that the coral is relatively rare below 20 m depth. The common depth range is currently observed at 5 to 15 m. In southeastern Florida, this species historically occurred on the outer reef platform (16 to 20 m) (Goldberg 1973), on spur and groove bank reefs and transitional reefs (Jaap 1984, Wheaton and Jaap 1988), and on octocoral-dominated hard-bottom (Davis 1982). In the Florida Keys *A. cervicornis* can occur from 1 to 34 m depths (Wells 1933, Davis 1982, Jaap 1984, Jaap and Wheaton 1988, Jaap et al. 1989). Colonies may also be common in back- and patch-reef habitats (Gilmore and Hall 1976, Cairns 1982). Although *A. cervicornis* colonies are sometimes found interspersed among colonies of *A. palmata*, they are generally in more protected, deeper water or seaward of the *A. palmata* zone and hence, protected from waves. Historically, *A. cervicornis* was the primary constructor of mid-depth (10 to 15 m) reef terraces in the western Caribbean, including Jamaica, the Cayman Islands, Belize, and some reefs along the eastern Yucatan peninsula (Adey 1978).

As depth increases, *A. cervicornis* colonies tend to be less compacted, have longer branches, and branching tends to be at greater intervals. Gladfelter (1982) demonstrated that infilling occurs as the branch elongates. Thus, at the tip, the porosity of the axial calyx is >90% and the wall is 60%, while at 60 cm from the tip, the porosity of the axial calyx is dead and the porosity of the wall is about 20%. This strengthens the branch as it elongates and the momentum of the branch increases. At depths of 20 to 40 m, where currents and wave force are minimal, branch diameter is thinner, being approximately half the diameter of a colony in the shallow surge zone. The porosity of the skeletons of *A. cervicornis* ranges from 35 to 65% by volume, with the mechanical strength of the skeleton proportional to the porosity (Schumacher and Plewka 1981). Because the skeleton is quite porous, it breaks readily in strong wave forces.

The growth rate for *A. cervicornis* has been reported to range from 3 to 11.5 cm/yr (Table 1). This growth rate is relatively fast in comparison to that of other corals and historically enabled the species to construct significant bioherms (reef structures) in several locations throughout the wider Caribbean (Adey 1978).

Table 1. The annual growth rate for *Acropora cervicornis* as reported from several sources.

Growth rate (cm/yr)	Location	Record
4	Dry Tortugas	Vaughan (1915)
10.9	Key Largo, Florida	Shinn (1966)
11.5	Eastern Sambo, Florida	Jaap (1974)
10	Key Largo, Florida	Shinn (1976)
7.1	U.S. Virgin Islands	Gladfelter et al. (1978)
3 to 4	Exuma, Bahamas	Becker and Muller (2001)

Gladfelter (1982, 1983a) used a scanning electron microscope to describe the growth process in *A. cervicornis*. She reported that crystals are initially deposited randomly on the distal margin of the axial corallite. Subsequently, needle-like crystals attach and grow outward from the surface of the crystals. The needle-like crystals in contact with the calicoblastic epithelial cells grow and fuse together generating the skeletal foundation or septotheca. During daylight, calcium carbonate accretion occurs on all of the skeletal elements; at night the activity is limited to fusiform crystal formation. Gladfelter (1983b) reported daily tissue growth of 300 µm in the region of the axial polyp. "*A. 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, Chalker and Taylor 1978, Gladfelter 1983b). Contrasting growth of in situ and laboratory-reared specimens revealed differences in the basal extension; however, other measurements (e.g., $CaCO_3$ accretion and vertical extension) were equivalent (Becker and Mueller 2001).

Growth in *A. cervicornis* is also expressed in expansion, occurring as a result of fragmenting and forming new centers of growth (Bak and Criens 1982, Tunnicliffe 1981). A broken off branch may be carried by waves and currents to a distant location or may land in close proximity to the original colony. If the location is favorable, branches grow into a new colony, expanding and occupying additional area. Fragmenting and expansion, coupled with a relatively fast growth rate, facilitates potential spatial competitive superiority for *A. cervicornis* relative to other corals and other benthic organisms (Shinn 1976, Neigel and Advise 1983, Jaap et al. 1989).
Fragments that contained the axial corallite were found to have lower mortality than fragments that came from the inner portions of a colony and did not have axial corallites (Bowden-Kerby 2001a). There was up to a six-fold difference in growth rate over 12 months based on the fragment's origin (Bowden-Kerby 2001b).

Acropora palmata

The maximum range in depth reported for *A. palmata* is <1 m to 30 m, but the optimal depth range for this coral is considered to be 1 to 5 m depth (Goreau and Wells 1967). Currently, the deepest known colonies of *A. palmata* occur at 21 m in the Flower Garden Banks National Marine Sanctuary (Hickerson pers. comm.) and at Navassa National Wildlife Refuge (Miller pers. comm.). The preferred habitat of *A. palmata* is the seaward face of a reef (turbulent shallow water), including the reef crest, and shallow spur and groove zone (Shinn 1963, Cairns 1982, Rogers et al. 1982). At low tide, colonies are sometimes exposed. Colonies of *A. palmata* often grow in nearly mono-specific, dense stands and form interlocking framework known as thickets in fringing and barrier reefs (Jaap 1984, Tomascik and Sander 1987, Wheaton and Jaap 1988). Storm-generated fragments are often found occupying back reef areas immediately landward of the reef flat/reef crest, while colonies are rare on lagoonal patch reefs (Dunne 1979). *Acropora palmata* formed extensive barrier-reef structures in Belize (Cairns 1982), the greater and lesser Corn Islands, Nicaragua (Gladfelter 1982, 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 5 m depth, with maximum water depths of framework construction ranging from 3 m to 12 m (see Table 1 in Lighty et al. 1982).

The growth rate of *A. palmata*, expressed as the linear extension of branches, is reported to range from 4 to 11 cm annually (Table 2) (Vaughan 1915, Jaap 1974). The 4-cm annual growth rate cited by Vaughan (1915) undoubtedly underestimates growth. Annual linear extension was estimated to be 8.8 cm; basal extension was 2.3 mm/month, and tissue growth was 200 cm^2 per month at Quintana Roo, Puerto Morelos, Mexico (Padilla and Lara 1996). A colony two meters in height could theoretically be 20 to 29 years old based on a 7 - to 10-cm annual growth rate. The theoretical age of a much larger colony (4 m) is 40 to 57 years old. Linear extension and tissue growth were dependent on the size of the colony; however, basal extension was independent of colony size (Padilla and Lara 1996). Colonies of *A. palmata* in the field had a greater calcification rate and rate of extension relative to specimens grown in an experimental tank (Becker and Mueller 2001). Wells (1933) reported from observations in 1932 that colonies of *A. palmata* were eight feet high (2.4 m) and 15 feet (4.5 m) in diameter at Bird Key Reef, Dry Tortugas; this is probably the maximum size that this species can attain.

Settled larvae typically create a small crust or patch with tubular corallites oriented at approximately 90 degrees from the plane of attachment. One or more protuberances develop and grow outward to form proto-branches.

Table 2. *Acropora palmata* growth rates reported from several sources.

Growth rate (cm/yr)	Location	Record
4	Dry Tortugas, Florida	Vaughan (1915)
10	Florida Keys	Jaap (1974)
4.7 to 9.9	U.S. Virgin Islands	Gladfelter, et al. (1978)
5.2	Colombia	Garcia et al. (1996)
2 to 11	Exuma, Bahamas	Becker and Mueller (2001)

The range of growth forms in *A. palmata* includes the iconic broad frond, with symmetrical colonies that are two or more meters across. Branches are up to 50 cm across and range in thickness from 4 to 5 cm, tapering toward the branch terminal; these colonies are most typical of the spur and groove formations where water circulation is omni-directional. In areas where wind and waves are predominantly from a single direction, the branches tend to grow in to the direction of the waves. The series of branches look like a medieval fortification (palisade); this growth form is typical of the barrier reef habitat. As depth increases, the branches are oriented in a more vertical orientation (Wainwright 1976, Graus et al. 1977). This compensates for hydraulic bending forces, but the thickening of the base also helps to counteract the hydrodynamic forces (Schumacher and Plewka 1981). *Acropora palmata* porosity ranges from approximately 35 to 45% by volume (Schumacher and Plewka 1981).

Acropora palmata can rapidly monopolize large areas by fragment propagation. A branch of *A. palmata* may be carried by waves and currents away from the mother colony to distances that range from 0.1 – 100 m, but usually less than 30 m (Baums et al. unpublished data). Fragments cleaved from the colony may grow into new colonies (Highsmith et al. 1980, Bak and Criens 1982, Highsmith 1982, Rogers et al. 1982). 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. 1991), Joan (Geister 1992, Zea et al. 1998), Gilbert (Kobluk and Lysenko 1992; Jordan-Dahlgren and Rodriguez-Martinez 1998), Andrew (Lirman and Fong 1996, 1997, Jaap pers. observ.), Georges and Charley (2004) (Jaap pers. observ.), as well as after Storms Bret (Van Veghel and Hoetjes 1995) and Gordon (Lirman and Fong 1997). Lirman and Fong (1997) reported that *A. palmata* fragment wounds healed rapidly (1.59 cm of linear growth/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.

Acropora prolifera

Acropora prolifera typically occurs in more protected back reef or lagoonal areas. Goreau and Wells (1967) list a depth range of 0 to 30 m, with 7 m depth considered optimal. On the north coast of Jamaica, Goreau (1959) noted occurrences in the rear zone, buttress zone, and fore reef terrace (*A. cervicornis* zone). In Belize, this coral was distributed seaward of the reef crest from 0.5 to 2 m depth (Cairns 1982). In the Florida Keys and Dry Tortugas, Davis (1982) and Wheaton and Jaap (1988) noted occurrences on bank reefs with spur and groove topography. The bases of *A. prolifera* colonies are often dead and detached from the substrate. Colonies of this species can be found growing in dense "thickets" with interlocking branches.

The reported growth rate for *A. prolifera* ranges from 3.7 cm (Vaughan 1915) to 8.2 cm per year (Gladfelter et al. 1978). This rate is approximately the same as for *A. cervicornis* (Table 1) and *A. palmata* (Table 2). The growth form is most like *A. cervicornis*; however, there is often a fan-like appearance on the terminal branches and a fusing of branches. *Acropora prolifera* also undergoes fragmentation and subsequent growth.

General Environmental Requirements

All Atlantic *Acropora* spp. are considered to be environmentally sensitive, requiring relatively clear, well-circulated water (Jaap et al. 1989). Atlantic *Acropora* spp. are almost entirely dependent upon sunlight for nourishment compared to massive, boulder-shaped species in the region (Porter 1976, Lewis 1977), with these latter types of corals more dependent on zooplankton. Thus, Atlantic *Acropora* spp. are much more susceptible to increases in water turbidity than some other coral species. Dredging or pollution activities that reduce long-term water clarity can also reduce the coral photosynthetic to respiration ratio (P/R ratio) below unity. Therefore, *Acropora* spp. may not be able to compensate with an alternate food source, such as zooplankton and suspended particulate matter, like other corals.

Optimal water temperatures for *A. palmata* range from 25 to 29°C, although colonies in the U.S.V.I. have been known to tolerate short-term temperatures around 30°C without obvious bleaching (loss of zooxanthellae). Jaap (1979) and Roberts et al. (1982) note an upper temperature tolerance of 35.8°C for *A. palmata*. All Atlantic acroporids are susceptible to bleaching due to adverse environmental conditions (Ghiold and Smith 1990, Williams and Bunkley-Williams 1990). Major mortality of *A. palmata* and *A. cervicornis* occurred in the Dry Tortugas, Florida, in 1977 due to a winter cold front that depressed surface water temperatures to 14 to 16°C. Some reduction in growth rates of *A. cervicornis* was reported in Florida when temperatures dropped to less than 26°C (Shinn 1966). All *Acropora* spp. require near oceanic salinities (34 to 37 ppt).

4.2 Reproduction/Recruitment

The distribution and abundance of Atlantic *Acropora* spp., like other coral species, reflects patterns of larval recruitment, asexual reproduction via fragmentation, mortality, regenerative capabilities, and aggressive interactions (Richmond and Hunter 1990). Inter-specific differences in the mechanisms of recruitment, dispersal, and mortality are likely important in determining the species composition of reef corals in different environments; such differences reflect the differential allocation of energy to the basic life history functions of growth (rate and rigidity of the skeleton), reproduction (fecundity, mode of larval dispersal, recruitment success), and colony maintenance (intra- and interspecific interactions, competitive ability, regeneration) (Connell 1973, Lang 1973, Bak and Engel 1979, Szmant 1986). Populations of Atlantic *Acropora* spp. are dependent upon sexual recruits for recovery after catastrophic disturbance, but can locally dominate hard-bottom and coral-reef habitats when colonies fragment and propagate across the bottom.

Extensive research has been conducted on the diverse reproductive strategies employed by scleractinian corals (Fadlallah 1983, Szmant 1986, Richmond and Hunter 1990). Atlantic *Acropora* spp., like many stony coral species, employ both sexual and asexual reproductive propagation. Sexual reproduction in corals includes gametogenesis (i.e., development of gametes) within the polyps near the base of the mesenteries. Some coral species have separate sexes, while others such as the Atlantic *Acropora* spp., are hermaphroditic. *Acropora cervicornis* and *A. palmata* in particular do not differ substantially in their sexual reproductive biology. Both species are spawners, meaning that coral larvae develop externally to the parental colonies (Szmant 1986) and both species are simultaneous hermaphrodites, meaning that a given colony will contain both female and male reproductive parts during the spawning season. Gametes (eggs and sperm) are located in different mesenteries of the same polyp (Soong 1991). The development period is longer for eggs than sperm, lasting approximately 10 months (Szmant 1986).

The spawning season for *A. cervicornis* and *A. palmata* is relatively short; with gametes released only a few nights during July, August, and/or September. In some populations, spawning is synchronous after the full moon during any of these three months. Annual egg production in *A. cervicornis* and *A. palmata* populations studied in Puerto Rico was estimated to be 600 to 800 eggs per cm^2 of living coral tissue (Szmant 1986). Eggs from both corals are ~300 µm in diameter. Colonies of *A. cervicornis* studied on the Caribbean coast of Panama during 1987-88 produced eggs 0.3 to 1.0 mm in length along the long axis that were elliptical in shape (Soong 1991). Spermaries were present during July and August and not during other times of the year. In the same study, *A. palmata* eggs were 0.2 to 1.0 mm in length along the long axis and shaped as irregular ellipses. Spermaries were present during July, August, and September. In a subsequent study, Soong and Lang (1992) observed that large axial polyps and basal tissues (1.0 to 4.5 cm from the colony base) in *A. cervicornis* were infertile, whereas gonads located within 2 to 6 cm of the branch tips always had smaller eggs than those in the mid-region of the branches. In *A. palmata*, small eggs were found in the whole colony, while infertile areas were observed in the encrusting base and along the growing edges of branches (Soong and Lang 1992). Upper surfaces of *A. palmata* colonies had significantly greater fecundity (more fertile polyps per unit surface area) and larger numbers of eggs within fertile polyps.

Colonies of *A. cervicornis* and *A. palmata* studied on the Caribbean coast of Panama indicated that larger colonies of both species (as measured by surface area of the live colony) have higher fertility rates (Soong and Lang 1992). For *A. palmata*, no colonies with a surface area between 4 and 15 cm^2 (n=4) or between 15 to 60 cm^2 (n=9) were fertile, while 7% of those 60 to 250 cm^2 in tissue surface area were fertile (n=14). Over 30% of the colonies between 250 and 1000 cm^2 in tissue surface area were fertile (n=16), 43% of colonies between 1000 and 4000 cm^2 (n=7), and 88% of colonies larger than 4000 cm^2 (n=33). In the same study, only colonies of *A. cervicornis* with a branch length larger than 9 cm were fertile, with 38% fertility for those 9 to 13 cm in branch length (n=13), 59% for 13 to 17 cm (n=17), and 89% for colonies with branches longer than 17 cm (n=18). Estimated size at puberty for *A. palmata* was 1600 cm^2 (n=84 colonies sampled) and for *A. cervicornis* was 17 cm in branch length (n=52 colonies sampled). The smallest reproductive colony of *A. palmata* was 16 x 8 cm^2 and for *A. cervicornis* was 9 cm in branch length (Soong and Lang 1992).

Acropora prolifera is a hybrid of *A. cervicornis* and *A. palmata*, and morphological variation is partially dependent upon which parental species provides the egg (Vollmer and Palumbi 2002).

In corals, fertilization can occur internally or externally, but in Atlantic *Acropora* spp., fertilization and development are exclusively external. Embryonic development culminates with the development of planktonic larvae called planulae (Photo 15). Little is known concerning the settlement patterns of planula larvae of Atlantic *Acropora* spp. (Bak et al. 1977, Sammarco 1980, Rylaarsdam 1983). In general, upon proper stimulation, coral larvae, whether released from parental colonies or developed in the water column external to the parental colonies, settle and metamorphose on appropriate substrates. Unlike most other coral larvae, *A. palmata* planulae appear to prefer to settle on upper, exposed surfaces, rather than in dark or cryptic ones (Szmant and Miller, accepted), at least in a laboratory setting. Initial calcification ensues with the forming of the basal plate and the initial protosepta, followed by the theca or polyp wall and axial skeletal members. Buds that form on the initial corallite develop into daughter corallites.

Both externally and internally produced coral planula larvae presumably experience considerable mortality (up to 90% or more) from predation or other factors prior to settlement and metamorphosis (Goreau et al. 1981). Once larvae are able to settle onto appropriate hard substrates, metabolic energy is diverted to colony growth and maintenance. Because newly settled corals barely protrude above the substrate, juveniles need to reach a certain size to reduce damage or mortality from impacts such as grazing, sediment burial, and algal overgrowth (Bak and Elgershuizen 1976, Birkeland 1977, Sammarco 1985). Recent studies examining early survivorship of lab cultured *A. palmata* settled onto experimental limestone plates and placed in the field indicate that survivorship is substantially higher than for *Montastraea faveolata*, another spawner, and similar to brooding species over the first nine months after settlement (Szmant and Miller, accepted). This pattern corresponds to the size of planulae; *A. palmata* eggs and larvae are much larger than those of *Montastraea* spp. Overall, older recruits (i.e., after they have survived to a size they are visible to the human eye, probably 1 to 2 yrs after settlement; see Photo 16) appear to have similar growth and post-settlement mortality rates across species (Van Moorsel 1988).

Photo 15. Planula larvae of *Acropora palmata* at a stage that is ready to settle. Photo credit A. Szmant.

Photo 16. *Acropora palmata* sexual recruit, St. John, U.S.V.I. Photo credit C. Rogers.

Spatial and temporal patterns of coral recruitment have been intensively studied on wider Caribbean reefs (Birkeland 1977, Bak and Engel 1979, Rogers et al. 1984, Baggett and Bright 1985, Chiappone and Sullivan 1996). Biological and physical factors that have been shown to affect spatial and temporal patterns of coral recruitment include substrate availability and community structure (Birkeland 1977), grazing pressure (Rogers et al. 1984, Sammarco 1985), fecundity, mode and timing of reproduction (Harriot 1985, Richmond and Hunter 1990), behavior of larvae (Lewis 1974, Goreau et al. 1981), hurricane disturbance (Hughes and Jackson 1985), physical oceanography (Baggett and Bright 1985, Fisk and Harriot 1990), the structure of established coral assemblages (Lewis 1974, Harriot 1985), and chemical cues (Morse et al. 1988). Relatively few studies, however, have examined variation in Caribbean coral recruitment over larger spatial scales (10 to 100 km) or among different structural types of reefs (Wallace and Bull 1981, Harriot and Fisk 1987, Fisk and Harriot 1990). In many studies of wider Caribbean reefs, a proxy measure of recruitment success has been the quantification of juvenile coral densities, with juvenile corals defined as metamorphosed corals visible underwater to the unaided eye ranging up to 4 cm in maximum diameter (Bak and Engel 1979). Newly settled corals are visible in the field at approximately 5 to 10 mm in diameter, and colonies approaching 4 cm in diameter are approximately 1 to 3 years old (Van Moorsel 1988).

Studies of *Acropora* spp. from across the wider Caribbean confirm two overall patterns of sexual recruitment: (1) Low juvenile densities relative to other coral species and (2) low juvenile densities relative to the commonness of adults (Porter 1987). This pattern suggests that the composition of the adult population is dependent upon variable recruitment. It also likely reflects the dominance of asexual reproduction by fragmentation for these species (i.e., surviving fragments are usually larger than 4 cm and thus never undergo a "juvenile" stage by this definition). In both Curaçao and Bonaire in the 1970's, densities of juvenile *A. palmata* reached 0.13 per m^2, while no *A. cervicornis* juveniles were found (Bak and Engel 1979). On the north coast of Jamaica, juvenile *A. cervicornis* densities were as high as 4.3 per m^2 at 11 m depth on barren substrate (Rylaarsdam 1983); however, phototransects revealed no *Acropora* spp. recruitment in 1976 or 1980 at <20 m depth, with smaller colonies presumably originating from larger colonies via fragmentation (Porter et al. 1981). In Salt River, St. Croix, *A. palmata* juveniles occurred at densities of 0.1 to 0.3 per m^2 at 3 to 9 m depth, while densities of juvenile *A. cervicornis* ranged from 0.01 to 0.30 per m^2 at 9 m depth (Rogers et al. 1984). Similar results were obtained in the Florida Keys (Dustan 1977, Porter and Meier 1992, Chiappone and Sullivan 1996). Surveys of nine sites representing three different offshore reef types from 3 to 15 m depth yielded no juveniles of *Acropora* spp. from 450, 1-m^2 quadrats (Chiappone and Sullivan 1996). To date, however, the settlement rates (number of larvae settling per unit area) of Atlantic *Acropora* spp. have still not been quantified; the juvenile density measurements cited above represent larvae that have not only settled, but metamorphosed (i.e., excreted a calcium carbonate skeleton) and survived to a specific size visible to surveyors underwater. Anecdotal evidence and observations in the wider Caribbean indicate that both *A. cervicornis* and *A. palmata* sexually recruit onto reefs, and in several instances, populations that have experienced major declines (>90%) are showing signs of recovery in terms of newly settled sexual recruits (Bruckner 2002).

Besides sexual reproduction, most coral species, including Atlantic acroporids, also reproduce asexually. Asexual reproduction involves fragmentation, wherein colony pieces or fragments are dislodged from larger colonies to form new colonies (Highsmith 1982). The budding of new polyps within a colony can also be considered asexual reproduction. Fragmentation can occur during storms (Porter et al. 1981, Tunnicliffe 1981, Highsmith 1982), with susceptibility to mechanical breakage of colony branches influenced by the boring activities of sponges and lithophagus bivalves. Fragmentation is a common means of propagation in many species of branching corals and historically has been considered to be the most common means of forming new colonies in Atlantic *Acropora* spp. (Gilmore and Hall 1976, Davis 1977, Tunnicliffe 1981, Bak and Criens 1982, Hughes 1985). The perception of the dominance of fragmentation as a reproductive mode for *A. palmata* and *A. cervicornis* implies that colonies derived from fragmentation can be distinguished from those derived from larvae. However, this may not always be the case. Recently developed genetic tools can detect colonies with the same genotype (implying one was fragmented from the other). Application of these tools in the field to a population of *A. palmata* (where individual small colonies were scored by field experts as larval or asexual recruits) indicated very poor correlation (Miller et al. in review). It appears that the reliability of assessing the contribution of sexual versus asexual reproduction in *Acropora* populations by field survey is limited, but is an area of study that warrants further investigation.

Asexual reproduction can play a major role in maintaining local populations when sexual recruitment is very limited. Fragmentation, followed by stabilization, survivorship, and growth can provide a mechanism for maintaining and expanding Atlantic *Acropora* spp. populations. However, region-wide declines have increased the reliance of *Acropora* spp. on sexual recruitment as a means of establishing and sustaining populations (Bruckner 2002). Atlantic *Acropora* spp. may require a certain storm frequency to maintain and expand populations through asexual reproduction, principally by fragmentation, when sexual recruitment is limited (Bruckner 2002). Frequent occurrence of storms or a single intense storm, however, may negatively impact colony survival, since a fragment may become abraded during the storm or may not encounter suitable substrate to reattach after the storm passes.

Implications of low Acropora spp. population size

Atlantic *Acropora* spp. are generally considered intermediate along the continuum from r-selected (rapid colonizers, fast growth, early maturation, but small maximum size and thus limited contribution to reef growth; generally brooding corals) to k-selected (slow growing, generally spawning, but attaining large colony size via indeterminate growth) life history strategies. *Acropora palmata* and *A. cervicornis* tend to be fast growing, have rapid wound healing, high rates of survival of asexually produced fragments, and the ability of broken branches to grow into new colonies (Gladfelter et al. 1978, Bak and Criens 1982, Highsmith 1982). Their level of aggression (i.e., ability to extend their mesenterial digestive filaments onto neighboring species and digest away living tissue) is relatively low compared to many other Caribbean corals (Lang 1973); however, Atlantic *Acropora* spp. have superior overgrowth capabilities. These life history characteristics, supported by documentation of recent trends in populations across the Caribbean, illustrate that once *Acropora* spp. experience local (reef-scale) reductions in colony numbers and size, recovery may not occur for decades.

There are several implications of the current low population sizes of *Acropora* spp. throughout much of the wider Caribbean. 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 *A. palmata* and *A. cervicornis* populations, given their state of drastically reduced abundance/density. Simultaneously, when adult abundances of *A. palmata* and *A. cervicornis* 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.

4.3 Population Genetics

Understanding the population structure of *A. cervicornis* and *A. palmata* is complicated by the fact that both corals undergo both sexual and asexual (clonal) reproduction (see section 4.2) and the relative contribution of each is not readily discernable in the field (Miller et al. in review). Two aspects of population structure are of critical importance in assessing extinction risk in widespread clonal species: (1) The degree of genotypic diversity (within populations and overall); and (2) the degree of genetic exchange between populations. The levels of genotypic diversity in *A. palmata* and *A. cervicornis* are of particular concern given their presumed dominant asexual reproductive mode (Highsmith 1982) and rapid range-wide decline (see section 4.5). That is, while quantitative field surveys may provide abundance estimates based on number of colonies or percent cover, it is conceivable that the genotypic diversity in either species might be drastically lower. The degree of genetic connectivity among populations is important in understanding the potential adaptation of local populations to specific environmental conditions and the potential for re-colonization from neighboring or distant reefs in areas of extirpation.

Immunological self-recognition (fusion versus rejection response when two individuals are placed in contact) was used in an early study to investigate clonal structure in *A. cervicornis* (Neigel and Avise 1983). This approach indicated that ramets of individual genets occurred at up to 20 m distance and individual genets occupied up to 10 m^2 in Jamaica and St. Croix, U.S.V.I. (Neigel and Avise 1983). However, there has been subsequent questioning of the genetic basis of the self-recognition response, as electrophoretically distinct individuals have been shown to fuse (e.g., Heyward and Stoddart 1985). Molecular genetic analysis seems to be necessary to reliably evaluate clonal structure.

Common molecular approaches to study genetic population structure such as mitochondrial DNA markers have yielded low levels of intraspecific variation in anthozoans in general and corals in particular and, hence, are of limited use in coral population genetic studies (Shearer et al. 2002). The presence of intracellular symbionts in coral tissue greatly complicates the application of highly polymorphic, anonymous DNA markers since it is difficult to distinguish between coral and symbiont DNA. Previous efforts at developing coral-specific microsatellite markers for *Acropora* spp. also met with little success (Marquez et al. 2000). Nonetheless, molecular genetic tools have recently become available to address questions of population genetic structure and gene flow in *A. palmata* (Baums et al. in press a) and *A. cervicornis* (Vollmer and Palumbi in prep), and are summarized below based upon manuscripts in development or under scientific review.

A recent study examined genetic exchange and clonal population structure in *A. palmata* by sampling and genotyping colonies from eleven locations throughout its geographic range using microsatellite markers (Baums et al. in press a). Results (Baums et al. in press b) indicate that populations in the eastern Caribbean (St. Vincent and the Grenadines, U.S.V.I., Curaçao, and Bonaire) have experienced little or no genetic exchange with populations in the western Caribbean (Bahamas, Florida, Mexico, Panama, Navassa, and Mona Island). Puerto Rico is an area of mixing where 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 (Baums et al. in press b).

The clonal structure of individual *A. palmata* populations was found to be highly variable, ranging from completely sexual where each colony represents a different genet to completely asexual, where all colonies comprise a single genet (Baums et al. in prep). The overall range-wide average, expressed as Ng/N (the number of genotypes found divided by the total number of colonies sampled) was about 0.5. Interestingly, clonal structure appeared to vary between the eastern and western Caribbean, with eastern populations being denser and more genotypically diverse (i.e., greater contribution by sexual recruitment) than western populations (Baums et al. in prep). In fact, four out of five populations sampled in the Florida Keys were monoclonal, indicating they were derived from fragmentation of a single larval recruit (Baums et al. in press (a) and unpublished data). This lack of genotypic diversity in several *A. palmata* populations implies that sexual reproduction may be completely lost and is thus a basis for concern for the long-term persistence of this species. Measures of genetic diversity such as heterozygosity are unknown for either species and are not likely to be revealed from the current genetic approaches.

Vollmer and Palumbi (in prep.) used DNA sequences of specific nuclear and mitochondrial genes, to analyze connectivity of *A. cervicornis* populations on a Caribbean-wide scale. Their results indicate a much finer scale of geographic differentiation (i.e., less connectivity across large areas) than the microsatellite results for *A. palmata* (Baums et al. in press b). They report that larval exchange between *A. cervicornis* populations as close as 2 to 15 km is extremely limited, implying that larval sources need to be conserved on a very small spatial scale. Little is known regarding clonal structure of *A. cervicornis* populations throughout their geographic range, although Vollmer and Palumbi (in prep.) indicate that approximately 60% of the colonies they sampled (purposely sampling colonies distant from each other) from areas throughout the Caribbean represented distinct genotypes. As in *A. palmata*, populations of *A. cervicornis* in southeast Florida (Broward County, probably the most abundant extant stands anywhere) appear to have low genotypic diversity as each of the large thickets sampled to date is monoclonal (Baums and Vargas unpubl. data).

4.4 Ecology/Ecosystem Function

Coral reefs serve a number of functional roles in subtropical and tropical environments of the wider Caribbean, including, but not limited to primary production, recycling of nutrients in relatively oligotrophic seas, calcium carbonate deposition yielding reef construction, refuge and foraging base for other organisms, and modification of near-field or local water circulation patterns (De Freese 1991). Coral reefs also protect shorelines, serving to buffer inshore subtidal (e.g., seagrass) and intertidal (e.g., mangroves) communities from otherwise high wave energy conditions in certain localities. Coral reefs are host to a multitude of species of algae, invertebrates, and fishes. Reef environments are characterized by an incredible diversity of species packed into a relatively small spatial dimension (m^2 to km^2) defined by high benthic diversity (Connell 1978, Richards and Lindeman 1987). Organisms essential in the construction of tropical reefs are hermatypic (reef-building) corals and coralline algae. Through reef construction, these organisms provide habitat for sedentary and mobile species (Lewis 1981).

The functional roles discussed below are presented for *Acropora* spp. where information specific to acroporids are available, and otherwise for coral reefs in general. This generalization to function in coral reef systems as a whole is appropriate in evaluating the role of *Acropora* spp. given their status as constructional or “foundation” species in Caribbean coral reef ecosystems as described below.

Acropora spp. were important shallow and mid-depth reef builders in the wider Caribbean

Acropora palmata and *A. cervicornis* are two of the major reef-building corals in the wider Caribbean. Historically, both of these species formed dense thickets at shallow (<5 m) and intermediate (10 to 15 m) depths in many reef systems, including some locations in the Florida Keys, western Caribbean (e.g., Jamaica, Cayman Islands, Caribbean Mexico, Belize), and eastern Caribbean. In the Florida Keys, for example, *A. palmata* was the primary builder of constructional spur and groove reefs along much of the Florida reef tract, with coralline spurs up to several meters in height and up to 15 m in length (Shinn 1963, Shinn et al. 1981). Early descriptions of Florida Keys reefs referred to reef zones, of which the elkhorn (*A. palmata*) zone was described for many shallow-water reefs (see Figure 2) (Jaap 1984, Dustan 1985, Dustan and Halas 1987). Interestingly, Shinn et al. (1977) noted that in southeastern Florida, some reefs were able to form and keep pace with sea level rise without the “help” of reef construction of *A. palmata*. As summarized in Bruckner (2002), however, the structural and ecological roles of Atlantic *Acropora* spp. in the wider

Caribbean are unique and cannot be filled by other reef-building corals in terms of accretion rates and the formation of structurally complex reefs.

Coral reefs influence water circulation patterns

An important characteristic of coral reefs is their ability to modify the surrounding physical-chemical environment (Ginsburg and Lowenstam 1958). The reef framework controls the accumulation of sediments on and adjacent to the reef, as well as local circulation patterns (Jaap 1984). Barrier reefs are the best example of the ability of organic communities to affect circulation patterns that in turn influence benthic community distribution and sedimentation. Barrier reefs provide shelter for the back reef lagoon, allowing for benthic communities adapted to low-wave energy conditions, such as seagrass beds, to persist and flourish. Several studies have noted the differences in sediment and habitat characteristics between inshore and offshore environments (Enos 1977, Szmant and Forrester 1996) and associated differences in sediment nutrient characteristics. Sediments in the back reef (inner shelf margin) consist of finer grain particles with greater nutrient pools relative to sediments directly associated with reefs, such as large skeletal fragments. Benthic community distribution also differs considerably between nearshore and offshore. Seagrasses and other soft-sediment communities dominate the inner shelf margin, while reefs and bare sand slope areas dominate the outer shelf margin.

Coral reefs serve important refuge and foraging functions

Coral reefs, including hard substrate and associated sediments, afford organisms an incredible array of refuges (Jaap 1984). Epifauna are organisms living on the reef surface, and include mobile epifauna (crustaceans, echinoderms, mollusks, and fishes) and sessile epifauna (e.g., sponges, corals, gorgonians, and bryozoans). Infauna are those animals which burrow into hard substrate, such as polychaete and sipunculid worms, sponges, and mollusks, while minute meiofauna are associated with reef sediments. Holes and crevices in the reef structure provide shelter for echinoderms, mollusks, polychaetes, crustaceans, other invertebrate groups, and fishes. In a single coral colony, for example, Grassle (1973) counted 1,441 polychaetes representing 103 species. In several coral colonies, McClosky (1970) counted 1,517 individuals representing 37 different invertebrate species. Gastropods, crustaceans, echinoderms, and fishes consume benthic algae associated with the reef structure (i.e., coral-produced substrate); these herbivores, in turn, fuel the production of higher trophic levels such as invertivores and carnivores.

While no comprehensive quantitative inventories have been made of all of the flora and fauna associated with coral reefs (Lewis 1981), probably the best information illustrating the diversity associated with these structures is for fishes. In western Atlantic reef environments, the number of fish species directly or indirectly associated with the reef system can exceed 400 species (Starck and Davis 1967, Jones and Thompson 1978, Bohnsack et al. 1987). The high taxonomic diversity of reef fishes indicates that many species are highly evolved, with several families entirely restricted to the reef environment, among them: Chaetodontidae (butterflyfishes), Scaridae (parrotfishes), Acanthuridae (surgeonfishes), Labridae (wrasses), Holocentridae (squirrelfishes), Balistidae (triggerfishes), and Pomacentridae (damselfishes) (Sale 1977, Longhurst and Pauly 1987). Many reef fishes are highly sedentary, with some species (e.g., damselfishes) actively defending territories. Even the spatial distribution of larger predatory species tends to be very reef-specific, with individuals rarely traveling more than 5 km from a home site after post-settlement, except for spawning purposes (Longhurst and Pauly 1987).

In addition to the important functions of reef building and reef maintenance provided by Atlantic *Acropora* spp., these species serve as fish habitat (Ogden and Ehrlich 1977, Appeldoorn et al. 1996), including essential fish habitat (CFMC 1998), for species of economic and ecologic importance. Loss of *Acropora* spp. from the wider Caribbean would have substantial impacts on many coral reef species and by extension on the composition of reef communities.

Assessments of reef fish abundances and diversity have been conducted in the Caribbean and the Florida Keys over the last four to five decades. Invariably, these studies have quantified fish populations relative to geomorphic strata or reef zonation (Ehrlich 1975, Sale 1980, McGehee 1994, Lindeman 1997, Kendall at al. 2003), or relative to substrate characteristics such as rugosity (Luckhurst and Luckhurst 1978), complexity (Nunez Lara and Arias Gonzalez 1998), or refuge (hole) size (Hixon and Beets 1989, 1993). A number of long-term sampling efforts may have data that can be used to infer habitat use or value, but these analyses have either not been published or are limited in spatial scope. However in St. Croix U.S.V.I., heterotypic schools of juvenile French and white grunts (*Haemulon flavolineatum* and *H. plumieri*) were found to transfer substantial amounts of nitrogen and phosphorous in the nutrient-poor waters of a coral reef; water nearby *A. palmata* with grunts had ammonia (NH^{4+}) concentrations up to 0.7 μM (micromolar) greater compared to a nearby colony without fish (Meyer et al. 1983). While direct connections between reef fishes and Atlantic *Acropora* spp. have not been well reported (with the exceptions below), several studies have found a positive relationship between substrate complexity and fish densities and diversity. Unfortunately, few of these studies provide data on the use of certain coral species or growth forms by particular fish species.

One exception to this pattern is the study by Lirman (1999) who reported significantly higher abundances of grunts (Haemulidae), snappers (Lutjanidae), and sweepers (Pempheridae) in high-topography areas with coverage by *A. palmata* compared to lower topography or lower coral cover sites. Comparisons between sites where *A. palmata* was absent and present suggested that fish schools, comprised primarily of grunts and snappers, use *A. palmata* colonies preferentially.

Settlement habitats of the white grunt, *Haemulon plumieri*, in another study were examined in southwest Puerto Rico in a *Thalassia-Acropora cervicornis* back-reef lagoon (Hill 2001). Although this site might nominally be classed as a seagrass bed, *A. cervicornis* was the primary focus of newly settling grunts. Neither the *Thalassia* (seagrass) nor other available coral sites (boulder or brain corals, gorgonians, algal covered corals) attracted or maintained significant numbers of juveniles during the study. Hill (2001) indicated that *A. cervicornis* thickets were the preferred settlement habitat for grunts that became saturated during high recruitment seasons, yielding greater usage of supposed sub-optimal habitats nearby (e.g., seagrass or gorgonians).

Numerous reef studies have described the relationship between increased habitat complexity, and increased species richness, abundance and diversity of fishes. Habitat selection is viewed as a trade-off between refuge from predation and access to feeding resources (Werner and Gillliam 1984). Settlement and juvenile habitats typically are thought to reduce exposure to predators (Shulman 1984). Hixon and Beets (1989, 1993) showed that appropriately sized refuges could moderate predation effects and thus alter reef fish distribution patterns. At a larger scale, complete absence of particular habitats has been shown to affect fish assemblage composition if species are not able to use alternate habitats (Nagelkerken et al. 2000). Loss of the complex habitats provided by *A. cervicornis* and *A. palmata* could result in increased rates of predation on juvenile snappers and grunts, with likely reductions of habitat-specifics like *H. plumieri*. It is important to note that *A. palmata* and *A. cervicornis* are the only large, branching coral species in Caribbean reef systems capable of creating large amounts of complex reef habitat. Though "standing dead" coral skeletons (especially *A. palmata,* as *A. cervicornis* tends to crumble into rubble) can still serve as habitat for fishes, subsequent storms and bioerosion will eventually destroy this habitat if none is being constructed to replace it. In the current situation, with low abundance of *Acropora* spp. on most Caribbean reefs, very little new complex reef habitat is being created and, hence, its availability to ecologically and economically important reef fishes is likely to continue to decline in the coming years.

4.5 Distribution and Abundance

This section presents an overview of *A. cervicornis* and *A. palmata* abundance and distribution (Figure 3) throughout the wider Caribbean, followed by case studies of relatively well-studied reef areas that have documented temporal patterns in percent coverage, density, size, and/or condition. Historical distribution and abundance patterns focus on percent coverage, density, and relative size of the corals during three periods: pre-1980, the 1980 – 1990 decade, and recent (since 2000). Few data are present before the 1980 baseline, likely due in part, to researchers' tendencies to neglect careful measurement of abundance of species that are ubiquitous.

When discussing historic distribution and abundance, it is important to briefly mention the environmental setting of the wider Caribbean (tropical western Atlantic, Caribbean-Atlantic province), insofar as environmental differences across the region influence the extent to which *Acropora* spp. have been able to build extensive reef structures. Specifically, although both *A. cervicornis* and *A. palmtata* are found throughout the Caribbean Sea, their historical abundance patterns are not necessarily similar and there is ample evidence to suggest that many reef systems were constructed without significant contributions by acroporids. Early reviews of western Atlantic reefs and coral species, as well as discussions of reef geomorphology in the western Atlantic, are provided elsewhere (e.g., Glynn 1973, Milliman 1973, Adey 1977; 1978), but provide context to the historical patterns of these corals.

Figure 3. Approximate range of *Acropora* spp. (highlighted), including the Gulf of Mexico, Atlantic Ocean and Caribbean Sea. The highlighted areas are not specific locations of the corals, rather reflect general distribution. Specific habitat information is provided in section 4.1.

The entire Caribbean-Atlantic province is characterized as microtidal and is impacted by largely unidirectional trade winds and waves subject, in part, to strong ocean flows. The most northern reefs in the province (i.e. Florida, northwestern Bahamas, and Bermuda) are cyclically stressed by the occasional effect of polar air during winter months and thus have limited reef development by *Acropora* spp. or lack these species altogether (Bermuda). Throughout the Caribbean, wave energy influences the degree to which crustose coralline algae and *Acropora* spp. dominate as reef-building elements (Adey 1977, Geister 1977). For example, large swells from the Atlantic Ocean limit acroporid reef development in the Windward Islands (eastern Caribbean) and the eastern flanks of the Bahamas (Roberts et al. 1992). In the Lesser Antilles, neither *A. cervicornis* nor *A. palmata* are significant agents of reef framework construction, due principally to higher wind strength, easterly consistencies, and longer fetch; this area is also subjected to long-period swells or rollers during the winter months that further limits shallow and mid-depth reef construction (Adey 1977). In the southwestern Caribbean (e.g., Panama), reef terraces are present that are potentially conducive to acroporid-reef development, but seasonally rough seas batter the area resulting in wave-swept pavements (Glynn 1973). In contrast, the northwestern Caribbean (e.g. Cuba, Cayman Islands, Jamaica, eastern Yucatan, Belize) is characterized by relatively low winds of medium to high easterly consistencies, that allows extensive acroporid growth at shallow and mid-depth (10 to 25 m). For example, the Belize Barrier Reef, the largest barrier reef in the province, appears to be based upon an *A. cervicornis* framework (Adey 1977).

The current range for both *A. cervicornis* and *A. palmata* remains unchanged from the historical (Figure 3) as far as data are available; there is a paucity of quantitative data for many locations throughout the wider Caribbean. Historically most data collected has been from a few specific reef sites that may or may not represent regional condition of the acroporids or coral reefs in general. In contrast, there are many qualitative data/observations indicating drastic declines in abundance of both *A. palmata* and *A. cervicornis* throughout their geographic range (e.g., Aronson and Precht 2001a).

Recently, there have been two publications that have summarized status (abundance and distribution) of *A. cervicornis* and *A. palmata*. The *Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program* (Lang 2003) provides results (1997–2004) of a regional systematic survey of corals, including *Acropora* spp., from many locations throughout the Caribbean (Figure 4). While data from this survey represent a snapshot in time of the reef, the geographic scope of the survey is great; targeted areas are visited by data collectors of varying expertise, and data represent a single survey. AGRRA data (1997-2004) indicate that the historic range of both species remains intact, that *A. cervicornis* is rarely found throughout the range (including areas of previously known occurrence) and a moderate occurrence of *A. palmata.*

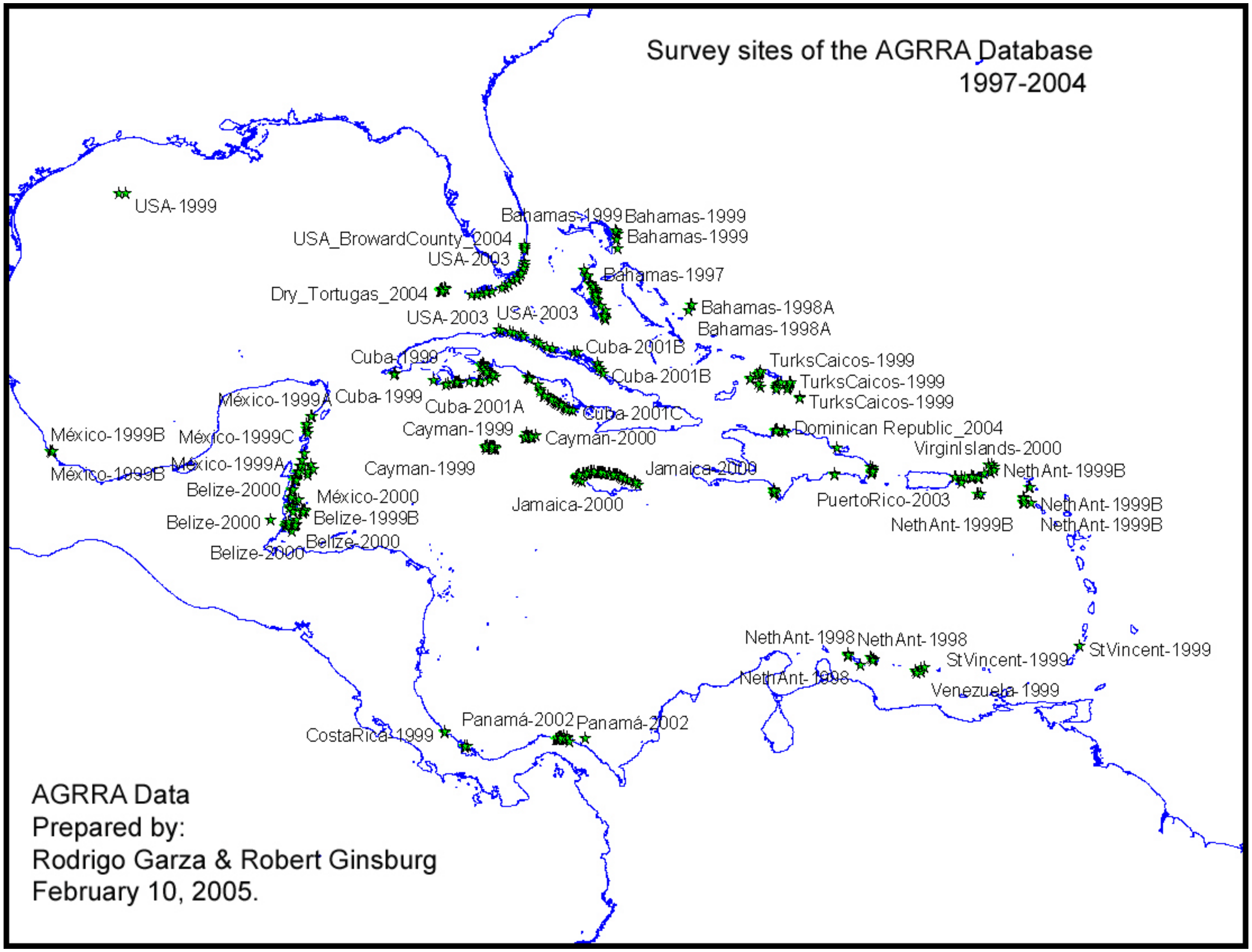


Figure 4. Location and year of AGRRA surveys from 1997-2004, representing surveys at ~800 sites in 22 areas across the Caribbean. Map provided courtesy Garza-Perez and Ginsburg.

An AGRRA bio-area index for *A. palmata* was recently developed to summarize data for nearly 300 sites throughout the wider Caribbean (Garza-Perez and Ginsburg pers. comm.). This bio-area index utilizes maximum diameter and partial mortality values of *A. palmata* colonies per site (total area of living tissue/10 transects) and is presented in Figures 5 and 6. Results from the spatial analysis are as follow:

1. most (n=61) bio-areas (Figure 5) ranked as moderate to high (100 to 500 m^2/10 transects) are concentrated in Andros Barrier Reef (Bahamas) and the northern Caribbean (Cuba and Belize);
2. 195 sites (Figure 6) distributed throughout the geographic area were ranked as low bio-areas (from 0.01 to 100 m^2/10 transects)
3. standing dead colonies of *A. palmata* were found throughout the geographic range (Figure 6).

It is important to note that the data for the Andros Barrier Reef AGRRA surveys were conducted prior to the Caribbean-wide 1998 coral die-off and the site has not been re-surveyed since 1997. Furthermore, status of *A. palmata* has not been updated following the 2004 hurricane season where Hurricanes Charley passed over Cuba, and Hurricanes Frances and Jeanne passed over the Bahamas.

Prior to the AGRRA summary, Bruckner (2002) provided a comprehensive summary of the best-known quantitative and qualitative data on the status of the Atlantic acroporids resulting from a NOAA-sponsored workshop wherein participants compiled data and summarized conditions throughout the range. Much of the data from the Bruckner 2002 report are summarized below, and some are updated and included in the case studies at the end of this section.

4.5.1 Abundance and distribution (historic and current) of *Acropora cervicornis*

Historically throughout much of the wider Caribbean, *A. cervicornis* so dominated the reef within the 7 to 15 m depth that the area became known as the staghorn zone (see Figure 2) and was documented as such in several reef systems such as the north coast of Jamaica (Goreau 1959) and the leeward coast of Bonaire (Scatteryday 1974). In many other reef systems in the wider Caribbean, most notably the western Caribbean areas of Jamaica, Cayman Islands, Belize and eastern Yucatan (Adey 1977), *A. cervicornis* was a major mid-depth (10 to 25 m) reef-builder. Principally due to wind conditions and rough seas, *A. cervicornis* has not been known to build extensive reef structures in the Lesser Antilles and southwestern Caribbean.

Bermuda

Historical surveys of the Bermuda platform indicate that *A. cervicornis* was absent (Garrett et al. 1971, Sterrer 1986), presumably due to low water temperatures associated with winter atmospheric cold fronts.

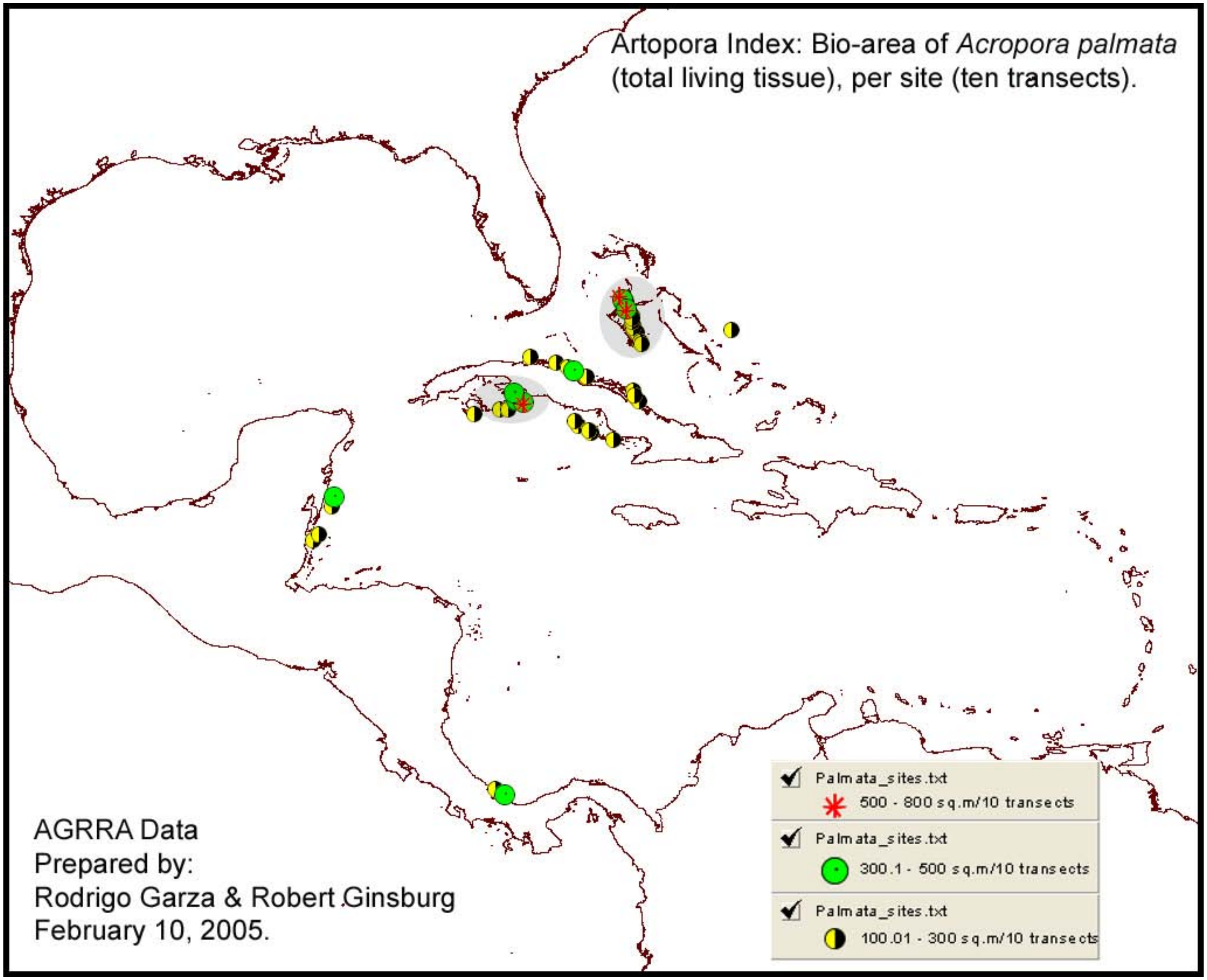


Figure 5. Locations of reefs indexed with moderate or high (circles) *Acropora palmata* bio-area as reported from 1997-2004 AGRRA surveys. Map provided courtesy Garza-Perez and Ginsburg.

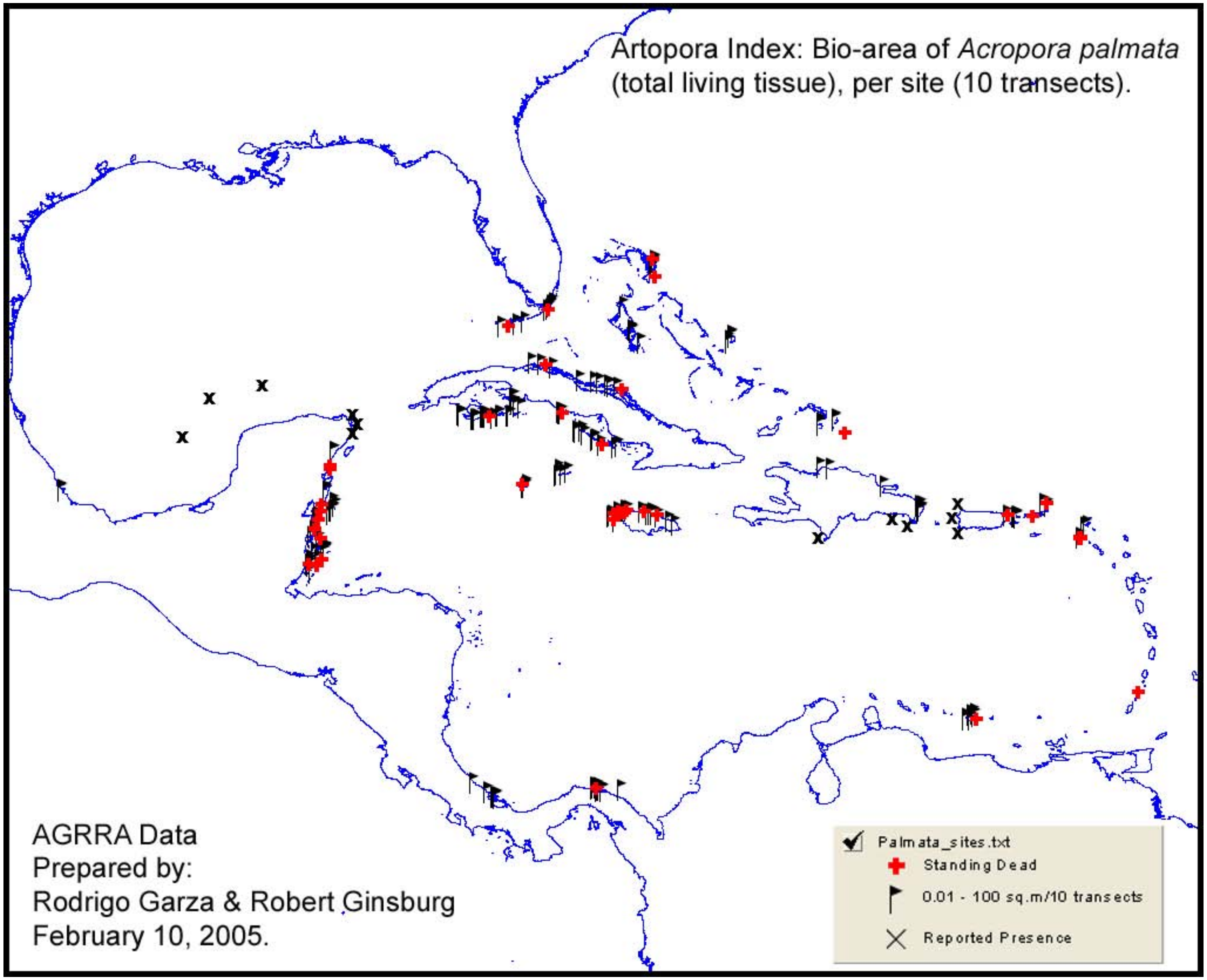


Figure 6. Locations of reefs indexed with low (flag) *Acropora palmata* bio-areas as reported from 1997-2004 AGRRA surveys. Locations of standing-dead *A. palmata* colonies are indicated by a cross. Map provided courtesy Garza-Perez and Ginsburg.

Southeast Florida

Acropora cervicornis has been documented as far north as Palm Beach (26^{o} 3'N) along Florida's east coast in deeper (16 to 30 m) water (Goldberg 1973) and is distributed further south and west throughout the coral and hard-bottom habitats of the Florida Keys (Jaap 1984). Distribution records for the southeast Florida coast include: Palm Beach (Goldberg 1973), the upper Florida Keys (Burns 1985, Dustan 1988, Dustan and Halas 1987, Jaap et al. 1988, Glynn et al. 1989), lower Florida Keys (Jaap and Wheaton 1975, Antonius et al. 1978, Wheaton and Jaap 1988), and Dry Tortugas (Vaughan 1915, Davis 1982, Dustan 1985, 1988, Jaap et al. 1989). In Biscayne National Park (Florida upper Keys) *A. cervicornis* was more abundant on reefs (e.g., Ajax and Long Reefs) further from tidal passes than those nearby, with historical coverage ranging from 0.1% to 2.7% in the 1980s (Burns 1985).

Because Florida is one of the few areas where multi-year quantitative data are available for *A. cervicornis* at more than a single location (Carysfort Reef; Dustan and Halas 1987, Looe Key Reef; Wheaton and Jaap 1988, Dry Tortugas; Davis 1982 and Porter et al. 1982), those data are further analyzed and presented as a case study in section 4.5.3.

Gulf of Mexico (west Florida shelf, Flower Gardens, southwestern Gulf)

No observations of *A. cervicornis* have been noted on the west Florida shelf, including the Florida Middle Grounds (Jaap et al. 1989). In the northwestern Gulf (Flower Gardens and associated banks), there are no historical records of *A. cervicornis* occurring in this area (Bright et al. 1984).

Numerous records for *A. cervicornis* in the southwestern Gulf of Mexico exist (e.g., Kuhlmann 1975, Farrell et al. 1983, Tunnell 1988); 38 emergent, platform-type coral reefs occur in the area (Tunnell 1992). A summary of qualitative data for the region follow:

- Kuhlmann (1975) surveyed reefs off Veracruz in 1965-66 and noted large thickets of *A. cervicornis*.
- Rannefeld (1972) surveyed Enmedio Reef and noted up to 100% cover by *A. cervicornis* in 1971; however, by 1987-91, coverage by this species declined to < 5% cover at Enmedio, Santiaguillo and Topatillo reefs, with the exact cause of mortality unknown (Tunnell 1992).
- Farrell et al. (1983) surveyed Cayos Arcas, Campeche Bank, and noted extensive monospecific stands of *A. cervicornis* on shallow reef flats. Interestingly, an earlier study (Logan 1969) did not document a monospecific stand at this site, suggesting that *A. cervicornis* proliferated at this site between the two surveys.
- Tunnell (1988) documented a mass mortality from a cold-water event on Lobos Reef (Veracruz) in 1977.

- During the summer of 1981, *A. cervicornis* thickets at 1 m depth on Topatillo Reef, Vercruz, were extirpated by freshwater inflow (Tunnell 1992).
- Tunnell (1988) stated that there was a marked decrease in coverage by *A. cervicornis* on upper reef slopes since 1973 in the southwestern Gulf, possibly caused by periodic river flooding and/or terrigenous sediment input. On leeward reef slopes, *A. cervicornis* dominated some southwestern Gulf reefs and was historically distributed on most major reef complexes in the area, including Veracruz, Blanquilla, Lobos, and Enmedio reefs.
- By the late 1980s, dead *A. cervicornis* remains were evident on the windward slopes of midshelf reefs off Veracruz (Enmedio, Rizo and Cabezo Reefs), as well as on the leeward slopes (Lara et al. 1992). While mass mortality had occurred by the late 1980s, *A. cervicornis* was still present in small numbers at six of the seven reef complexes surveyed offshore of Veracruz and was present in nine of the 10 reef complexes off Anton Lizardo (Lara et al. 1992).

Bahamas and Turks and Caicos Islands

Distribution records of *A. cervicornis* in the Bahamas include: Great Bahama Bank (Reed 1985), offshore of Grand Bahama Island (Jaap et al. 1989), and the Turks and Caicos (Sullivan et al. 1994, Chiappone et al. 1996). In the Turks and Caicos Islands (southeastern Bahamas), *A. cervicornis* was recorded on all types of reefs (i.e., patch, transitional, and both high-and low-relief spur and groove) in depths of 1 to 15 m (Sullivan et al. 1994); however colony densities were very low (< 0.5 per m^2) and coverage was < 1%. Nearby on the eastern margin of the Turks and Caicos Bank, Chiappone et al. (1996) sampled 13 patch and fringing reefs in depths 1 to 30 m and found that *A. cervicornis* was locally abundant on some patch reefs on the bank, but did not form extensive thickets. They concluded that the turbulence from heavy winter seas in the southeastern Bahamas limits *A. cervicornis* from forming extensive thickets on mid-depth reefs.

Greater Antilles (Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, U.S. Virgin Islands)

Cuba

Historical distribution records for *A. cervicornis* on the island shelf of Cuba are detailed in Zlatarskia and Estalella (1982). In addition, data from ten shallow-water reefs located on the southeastern coast had localized patches of *A. cervicornis* on mid-depth spur and groove reefs (6 to 13 m depth), with coverage up to 9% (Chiappone et al. 1996).

Cayman Islands

Historical distribution records for the Cayman Islands (Grand Cayman, Little Cayman, Cayman Brac) include Roberts (1971) and Ghiold and Smith (1990). *Acropora cervicornis* was historically abundant on shallow-water reefs within North Sound, Grand

Cayman, specifically in the moat zone (2 to 4 m) with head corals and gorgonians, but also on sand flats during (Roberts 1971). About 20 years later, Fenner (1993) characterized *A. cervicornis* as occurring intermediate (between rare and common) on Cayman Brac and Little Cayman.

Jamaica

Because Jamaica is one of the few areas where multi-year quantitative data are available, those data are further analyzed and presented as a case study in section 4.5.3.

Hispaniola (Haiti and Dominican Republic)

No historical data are available describing the distribution or abundance of *A. cervicornis* in either Haiti or the Dominican Republic. A recent report from the Dominican Republic describes *A. cervicornis* as common in some areas within the national parks (i.e., deep water, reef lagoon, flat- and back-reefs), however, in other areas such as the offshore banks, only rubble and dead standing colonies are found (Geraldes 2002).

Puerto Rico:

In Puerto Rico, well-developed and dense thickets of *A. cervicornis* were present through the late 1970s at many reefs surrounding the main island, and also the offshore islands of Mona, Vieques and Culebra (Almy and Carrión-Torres 1963, McKenzie and Benton 1972, Rogers 1977, Goenaga and Cintrón 1979, Boulon 1980). Later, in 1978-79 during an island-wide survey, *A. cervicornis* was found on only 20% of those reefs (Bruckner 2002).

Unfortunately quantitative trend data sufficient for a case study to depict trend in *A. cervicornis* abundance or distribution are not available from Puerto Rico. A recent description of the status of *A. cervicornis* in Puerto Rico can be found in Bruckner (2002); a few other studies are summarized below:

- Along the shelf-edge reef south of Puerto Rico, *A. cervicornis* was the dominant coral prior to Hurricane David in 1979. Twenty random 0.6 m^2 photoquadrats were selected from each of ten 40-m long transects parallel to the depth contours across the reef (16.7 to 19.2 m depth). Based on analysis of point count data, *A. cervicornis* had a mean of 31.1% total cover (range of 9.9 to 56.9%) prior to the storm; after the storm, total cover of *A. cervicornis* dropped to a mean of 0.90% (range of 0.02 to 2.7%) (Boulon unpubl. data).
- With the exception of a few reefs in the southwest and isolated offshore locations, the dense, high profile, monospecific thickets of both species (*A. cervicornis* and *A. palmata*) have disappeared from Puerto Rico coral reefs (Weil et al. unpublished data).
- In the summer of 2004, there was an epidemic outbreak of white pox disease at Los Corchos coral reef in Culebra, Puerto Rico. Coral cover on the reef reaches values of 80%; a total of 80 to 90% of the *A. cervicornis* colonies at a permanent monitoring site were already dead or dying three weeks after Tropical Storm Jeanne (Rogers, pers. comm.).

U.S. Virgin Islands
Because the U.S. Virgin Islands is one of the few areas where multi-year quantitative data are available, those data are further analyzed and presented as a case study in section 4.5.3.

Lesser Antilles (British Virgin Islands and south)

Presumably due to heavy swell, *A. cervicornis* was not historically an important mid-depth reef builder (Adey and Burke 1977), although it was present on the insular shelves of many islands in the eastern Caribbean, including the British Virgin Islands (Dunne and Brown 1979), Martinique (Adey et al. 1977), St. Lucia (Roberts 1972), and St. Vincent (Adams 1968) south to Barbados and Grenada. At Anegada (British Virgin Islands), *A. cervicornis* was common in the lagoon and rear zone of Jack Bay, abundant in the rear zone at East end, and rare to abundant on leeward patch reefs in the 1970s (Dunne and Brown 1979). On Saba, surveys at a CARICOMP station within the marine park suggested that coverage by dominant coral species, including *A. cervicornis*, was relatively stable in the early 1990s, with bleaching and hurricane damage considered the principal threats (Smith and Ogden 1994). In Martinique, *A. cervicornis* historically was rare on the eastern (windward side) of the island (Adey et al. 1977). Reefs in St. Lucia (between Martinique and St. Vincent) are located primarily along the windward eastern coast (Roberts 1972) and *A. cervicornis* was predominant in the 6 to 8 m depth with thickets of colonies reaching 1 to 1.5 m in height (Roberts 1972). Although present in St. Vincent, this coral did not form a staghorn zone on the insular shelf (Adams 1968). *Acropora cervicornis* was documented in the Tobago Cays of the Grenadines in the 1970s (Lewis 1975).

Continental Caribbean (eastern Yucatan to northern coast of South America)

Distribution records for the eastern Yucatan peninsula, Mexico, include Jordan et al. (1981), Moreno et al. (1981), and Fenner (1988). Along northeastern Yucatan peninsula during late the1970s, *A. cervicornis* had 28% or greater coverage in the rear zone and more than 48% cover on the deeper (10 m) fore-reef at several locations (Moreno et al. 1981). *Acropora cervicornis* on the leeward side of the island of Cozumel was characterized by Fenner (1988) as relatively rare; this area historically lacked dense stands of either *A. cervicornis* or *A. palmata*, with *Agaricia tenuifolia* (*A. agaricites* forma *bifaciata*) dominating intermediate depths (Fenner 1988) similar to some reefs of Costa Rica (Cortes and Risk 1984), Belize (Rutzler and Macintyre 1982) and Grand Cayman.

Belize
Although few records exist describing *A. cervicornis* distribution in Belize, the species was historically common (thickets) in the sand trough and outer ridge of the Carrie Bow Cay outer fore-reef (Cairns 1982), and at a CARICOMP monitoring station that characterized *A. cervicornis* as one of the dominant corals with cover being relatively stable in the early 1990s (Smith and Ogden 1994). *Acropora cervicornis* was considered

one of the 10 most common corals from surveys of back- (< 1.5 m) and fore-reef (6 to 15 m) habitats at 13 locations from Ambergris Caye south to Placentia (McField 1999).

Honduras

Acropora cervicornis was characterized as intermediate (between rare and common) on fringing reefs offshore of Roatan during the late 1980s (Fenner 1993). Distribution records also include:

- Cayos Cochinos, Bay Islands, during 1994-96 (Guzman 1998), and
- Isolated colonies were recorded at 5 m depth on windward sides of islands (Ogden and Ogden 1998), as well as on some leeward sites, with evidence of white band disease. A*cropora cervicornis* was affected by a 1995 bleaching event in Cayos Cochinos, Guzman and Guevara 1998.

Nicaragua

Surveys at Albuquerque and Courtown atolls (200 km east offshore Nicaragua) revealed that *A. cervicornis* was conspicuous on patch reefs in the lagoon zone from 3 to 5 m depth (Diaz et al. 1996).

Costa Rica

Acropora cervicornis was historically restricted to the reef complex at Cahuita, Costa Rica (Cortes and Guzman 1985a; b).

Panama

Distribution records for the Caribbean coast of Panama include Galeta Reef (Porter 1972, Cubit and Williams 1983).

Colombia

Distribution records for *A. cervicornis* in Colombia include surveys by Erhardt and Werding (1975), Ramirez et al. (1985), and Liddell and Ohlhorst (1988). Mass mortality of *A. cervicornis* throughout the Caribbean coast of Colombia apparently occurred by 1980 as areas of dead stands (coverage only up to 0.1%); mortality was partially attributed to bleaching (Ramirez et al. 1985). Dead stands of *A. cervicornis* were noted on the sandy reef platform (0 to 7 m) and fore reef terrace (2 to 9 m) at Tesoro Island, Rosario Archipelago in 1992, with dead colonies in upright position and covered with algae (Sanchez 1995). The CARICOMP station at Chenque Bay noted *A. cervicornis* as the dominant coral species in 1992, but with a trend in declining cover due to disease, bleaching, and dynamite fishing (Smith and Ogden 1994).

Venezuela

Earliest historic At Los Roques National Park, Venezuela, maximum dominance of *A. cervicornis* (18% of live cover and 9% of all colonies) was reported on the fore-reef terrace(3-6 m) with numerous dead fragments (Sandia and Medina 1987) but not documented elsewhere offshore of Venezuela (Liddell and Ohlhorst 1988). Nearby in Trinidad, *A. cervicornis* was noted at one site during the 1970s (Kenny 1988). Further west in the Netherlands Antilles (Islands of Aruba, Bonaire, Curaçao), distribution records include those from Roos (1971), Scatterday (1974) and Bak (1977). Surveys conducted by Roos (1971) during 1961 at 17 locations around the Curaçao coastline including most sites on the western coast did not record *A. cervicornis* in the inner bays. On the island shelf of Bonaire, reefs are restricted primarily to the leeward coast due to heavy surf conditions; a mid-depth dominance by *A. cervicornis* in the *A. cervicornis*- *M. annularis* zone was noted in the 1970s (Scatterday 1974). Dense thickets of colonies historically occurred sporadically on the leeward coast of Curacao; northwest of Piscadera Bay *A. cervicornis* coverage was <1% during the 1970s from 2 to 14 m depth (Bak 1977).

Further east to Brazil, no distribution records exist for *A. cervicornis* (Leao 1986, Leao et al. 1988); the genus *Acropora* is absent south of the equator in the Atlantic region (Glynn 1973).

4.5.2 Historical and current distribution and abundance of *Acropora palmata*

Throughout much of the wider Caribbean, *A. palmata* historically comprised the elkhorn zone (see Figure 2) at 1 to 8 m depth (reef flat, wave zone, reef crest) in diverse areas as Jamaica (Goreau 1959), Alacran Reef, Yucatan peninsula (Kornicker and Boyd 1962), Abaco Island, Bahamas (Storr 1964), the southwestern Gulf of Mexico, Bonaire (Scatterday 1974), and the Florida Keys (Jaap 1984, Dustan and Halas 1987). The predominance of *A. palmata* in shallow reef zones is related to the degree of wave energy; in areas with strong wave energy conditions only isolated colonies may occur, while thickets may develop at intermediate wave energy conditions (Geister 1977). Although considered a turbulent water species, *A. palmata* is sensitive to breakage by wave action, and is thus replaced by coralline algae in heavy surf zones throughout the province (Adey 1977).

Bermuda

No historical distribution records exist for *A. palmata* on the Bermuda platform (Garrett et al. 1971, Sterrer 1986).

Southeast Florida

While *A. cervicornis* has been documented further north along the Florida east coast, the northern extension of *A. palmata* is at Fowey Rocks offshore the Miami area (25^{o} 37’ N) (Porter 1987). This area technically begins the Florida Reef Tract where all of the major reef-building corals appear in shallow water in the southeastern U.S. (Burns 1985). Surveys in the early 1970s north of Miami (e.g., Palm Beach) did not note the occurrence of *A. palmata* (Goldberg 1973). Between Fowey Rocks and Carysfort Reef, *A. palmata* has been historically rare as the significant reef development or framework construction by *A. palmata* begins further south at Carysfort Reef (25^{o} 20’N), extending discontinuously southwestward to the Dry Tortugas (Jaap 1984). Notably, recent surveys have reported a few colonies of *A. palmata* off Pompano Beach, Broward County, FL (Photo 17).

Distribution records of *A. palmata* for the southeast Florida coast include: upper Florida Keys (Burns 1985, Dustan 1985; 1988, Dustan and Halas 1987, Jaap et al. 1988), lower Florida Keys (Jaap and Wheaton 1975, Antonius et al. 1978, Jaap 1979, Wheaton and Jaap 1988), and Dry Tortugas (Davis 1982, Jaap et al. 1989). Offshore reefs built primarily by *A. palmata* are situated along the outer margin of an arc-shaped limestone plateau (south Florida shelf). "Flourishing" *A. palmata* reefs (i.e., those with a shallow or emergent reef flat) are limited to the northern seaward half of Key Largo where an *Acropora* zone (reef flat/reef crest) was present. At Molasses Reef (nearby Key Largo), living *A. palmata* was almost absent in 1959-60 (Shinn 1963) and it was later suggested that conditions necessary for the growth of this coral changed since the coralline spurs were originally accreted (Shinn et al. 1981).

Photo 17. *Acropora palmata* off of Pompano Beach, Broward County, Florida in 2003; status of these few northern-most colonies presently is unknown. Photo credit J. Sprung.

Numerous other studies describing *A. palmata* abundance and distribution in the Florida Keys are available. When possible, data (e.g., Chiappone and Sullivan 1997) were further analyzed and presented as a case study in section 4.5.3. Other data from shorter-term projects throughout the Florida Keys are summarized below:

- Changes in coral communities on six reefs at two depths from 1984 to 1991 (including sites in both the upper Keys and lower Keys) noted a decline in *A. palmata* abundance at shallow depths (4 to 6 m) but not deeper (Porter and Meier 1992). These changes were attributed to disease and the demise of the long-spined sea urchin (*Diadema antillarum*).
- Living and dead assemblages of corals on two offshore sites and two patch reefs were compared and significant differences in taxonomic composition

between live and dead coral assemblages were found between reef types (Greenstein and Pandolfi 1997). While both the patch and offshore reefs historically had more *A. cervicornis* and *A. palmata*, they were now dominated by other corals (*Porites astreoides* and *Siderastrea sidereal*). Interestingly, massive growth forms were under-represented in the dead assemblage, while branching growth forms (*Acropora* spp.) were under-represented in the live coral assemblage.

Gulf of Mexico (west Florida shelf, Flower Gardens, southwestern Gulf)

No observations of *A. palmata* have been noted on the west Florida shelf, including the Florida Middle Grounds (Jaap et al. 1989). Historically *A. palmata* was not known to occur in the northwestern Gulf of Mexico, including the Flower Garden Banks (Bright et al. 1984). However, reconnaissance dives in 2003 havereported the presence of an *A. palmata* colony at 71 ft of depth.

Numerous records of *A. palmata* in the southwestern Gulf of Mexico exist (e.g., Farrell et al. 1983, Tunnell 1988, Ferre-D'Amare 1988); 38 emergent, platform-type coral reefs occur in the area (Tunnell 1992). Distribution/abundance records for *A. palmata* in this area include:

- *Acropora palmata* was historically known from most major reefs in the southwestern Gulf, including Veracruz, Blanquilla, Lobos, and Enmedio reefs (Tunnell 1988).
- *Acropora palmata* historically occurred on the leeward sides of bank reefs off Tampico and Veracruz and was referred to as "absolutely dominant in shallow water" (Ferre-D'Amare 1988).
- Kuhlmann (1975) surveyed reefs off Veracruz in 1965-66 and noted an *A. palmata* zone on several offshore bank reefs. Within the *A. palmata* zone, coverage by this species from 0.5 to 10 m depth ranged from 15 to 65% at four different reefs off Veracruz during 1965-66 and 1971 (Kuhlmann 1975, Rannefeld 1972).
- At Enmedio Reef, coverage by this species ranged from 5 to 50%, but declined to 1.4% at Enmedio and to 3% at Cabezo reefs by 1989 (Tunnell 1992), with the exact cause of death unknown.
- Extensive monospecific stands of *A. cervicornis* on shallow reef flats, followed by *A. palmata* in deeper depths (reverse of typical Caribbean pattern) were found by Farrell et al. (1983) at surveyed Cayos Arcas, Campeche Bank.
- A cold-water event led to mortality on Lobos Reef (Veracruz) in 1977, with marked decreases in coverage by *A. palmata* on upper reef slopes (relative to 1973) possibly caused by periodic river flooding and/or terrigenous sediments (Tunnell 1988).
- In the 1980s, the windward fore reef zone of southwestern Gulf reefs (8 to 10 m depth) did not exhibit extensive growth of *A. palmata* as they once did and dead stumps were common. *Acropora palmata* was considered common in the late 1980s in reef lagoon areas off shore of Veracruz at 0.5 to 2 m depth

(Lara et al. 1992). It was also relatively abundant on fore-reef edge in some areas of heavy turbulence, as well as the inner fore reef. Surveys of several reef complexes in the southwestern Gulf by Lara et al. (1992) indicated that *A. palmata* was present on five of the seven reef complexes off of Veracruz and nine of the ten reef complexes off Anton Lizardo in the late 1980s.

- Some recovery of *A. palmata* in the late 1980s and early 1990s was noted in the southwestern (Gulf Jordan-Dahlgren 1992). Healthy stands of *A. palmata* predominated the Veracruz reef system until the late 1960s, then in 1971 the first report of mass mortality was reported at Enmedio Reef (Rannefeld 1972). The condition of the corals gradually worsened through the 1970s until recolonization was noted at several reefs in the late 1980s; recolonization was greater southward and further offshore of Veracruz on dead *A. palmata* skeletons. These recovery patterns "suggest that the species' demise may not have been an extraordinary event in the history of these reefs" (Jordan-Dahlgren 1992).

Bahamas and Turks and Caicos Islands

Acropora palmata historically dominated reef crest environments on Great and Little Bahama Banks, such as Abaco Island (Newell et al. 1959, Storr 1964). In the Turks and Caicos Islands, *A. palmata* was distributed on patch reefs (1 to 1.5 m) on the southeast platform margin of Caicos Bank near South Caicos in 1991 (Sullivan et al. 1994); with an absence of reef flat or reef crest development by this species on the eastern, windward margin. In the Caicos Bank, *A. palmata* was locally abundant in 1991 on some eastern patch reefs in depth from 1 to 30 m (Chiappone et al. 1996). Diseased *A. palmata* was common in San Salvador by the 1980s (Dustan 1994). Recently (Shelten et al. 2005) found *A. palmata's* populations in South Caicos in good condition with living tissue on individual colonies (75.9%) being significantly greater than at thickets (58.6%) and old skeleton (22.7 to 38.0%) and little incidence of disease.

Greater Antilles (Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, U.S. Virgin Islands)

Cuba

Distribution records for the island shelf of Cuba include Kuhlmann (1974) and Zlatarski and Estalella (1982). This species historically (1960s and 1970s) occurred on lagoon reef flats, spur and groove, reef slope, and bank reef environments (Kuhlmann 1974) and dominated reef flat communities on barrier reefs (Zlatarski and Estalella 1982). The *A. palmata* framework on shallow-water reefs (> 5 m depth) on southeastern coast was mostly dead with coverage about 2 to 3% (Chiappone et al. 1996).

Cayman Islands

Historical distribution records for the Cayman Islands include Roberts (1971), Ghiold and Smith (1990) and Fenner (1993). *Acropora palmata* historically dominated shallow-water reefs within North Sound, Grand Cayman (Roberts 1971) and was the dominant coral on the reef crest during 1967. By the late 1980s, this coral was characterized as intermediate (between rare and common) on Cayman Brac and Little Cayman (Fenner 1993).

Jamaica

Because Jamaica is one of the few areas where multi-year quantitative data are available, those data are further analyzed and presented as a case study in section 4.5.3.

Hispaniola (Haiti and Dominican Republic)

Few data describing historical distribution and abundance of *A. palmata* exist. Geraldes (2002) reported that condition of *A. palmata* in the Dominican Republic varied depending on the location within the fringing reef system. *Acropora palmata* was common in deep water and within the national parks on the reef flat and back reefs; in other habitats only dead colonies were found, some being overgrowth by algae (Geraldes 2002).

Puerto Rico:

Extensive thickets of *A. palmata* were present in 40% of 35 sites surveyed around the island of Puerto Rico in the late 1970s (summarized in Bruckner 2002). These populations were impacted by various stressors in the 1980s: large stands of *A. palmata* on east coast reefs near Fajardo were decimated by WBD in the mid 1980s, followed by Hurricane Hugo in 1989 that resulted in nearly total destruction of the remaining thickets (Goenaga and Boulon 1992).

Currently, large stands of dead *A. palmata* occur on the fringing coral reefs along the shoreline of Puerto Rico (i.e., Punta Picúa, Punta Miquillo; Río Grande, Guánica, La Parguera, Mayagüez). Because the *A. palmata* skeletons remain in their upright growth position, mortality is thought to have been caused by factors such as disease, bleaching, sedimentation, algal competition, or any combination, and not from physical damage associated with storms or hurricanes.

U.S. Virgin Islands

Because the U.S. Virgin Islands is one of the few areas where multi-year quantitative data are available, those data are further analyzed and presented as a case study in section 4.5.3.

Lesser Antilles (British Virgin Islands and south)

Historically, *A. palmata* was an important framework builder in water depths less than 6 m in the Lesser Antilles (Virgin Islands south to Grenada) (Adey and Burke 1977). Offshore of Anegada, British Virgin Islands, *A. palmata* was rare to common in the rear zone, but abundant on reef tops and leeward patch reefs (Dunne and Brown 1979). A CARICOMP station within a Saba marine park noted *A. palmata* as one of the dominant coral species, with coverage characterized as relatively stable in the early 1990s (Smith and Ogden 1994).

Carbon-14 dating of bank barrier reefs in Martinique indicated a shift in dominance from *A. palmata* to fleshy algal domination (Adey et al. 1977). Reconnaissance surveys from the Virgin Islands to Grenada during the 1970s indicated approximately 36% of the approximately 800 km of available windward coast were *A. palmata* reefs (Adey et al. 1977). Historically *A. palmata* also dominated shallow protected areas (Bouchon et al. 1985).

Reefs off St. Lucia are located primarily along windward eastern coast in the northernmost Windward Islands (Roberts 1972) situated between Martinique and St. Vincent. Data from this area during the 1970s indicate that while *A. palmata* was a conspicuous component of fringing reefs, it was not dominant like *Porites astreoides* and *Diploria clivosa* on the southeastern side of the island (Roberts 1972). Meanwhile on the southern coast (Anse Gallette region) of St. Lucia, *A. palmata* constructed a *palmata* zone (1 to 5 m depth), forming interlocking thickets with colonies up to 2 m in height.

In the Grenadines (Tobago Cays), *A. palmata* was present on Horseshoe Reef, including the seaward limit of the back reef (1 to 2 m depth) (Lewis 1975). Historically, *A. palmata* dominated the reef crest (1 to 2 m depth), and the benthos was covered with branches broken from the colony during heavy wave action and turbulence (Lewis 1975). *Acropora palmata* also occupied the inner edge of the reef front seaward of reef crest. Near Carriacou in the Grenadines, Goodwin et al. (1976) sampled Jack Adam Island and Saline Island, north and south of Carriacou, respectively, and found that small fringing reefs historically had abundant *A. palmata*. Off the island of St. Vincent, between Grenada and St. Lucia, the reef crest and shallow fore reef slope were historically dominated by *Porites* instead of *A. palmata* (Adams 1968). *A. palmata* historically occupied the reef crest (*Millepora* zone) at 1 m depth and was best developed in this zone relative to the back reef and fore reef environments (Adams 1968).

Continental Caribbean (eastern Yucatan to northern coast of South America)

Distribution records for *A. palmata* off the eastern Yucatan peninsula, Mexico, include Jordan et al. (1981), Moreno et al. (1981), and Fenner (1988). In the 1970s, coverage of *A. palmata* along the northeastern Yucatan peninsula was 28 to 48% in the rear zone and at 5 m depth on the fore reef and was nearly 50% at some reefs, while dominating the shallowest part of reef profile (0.6 to 1 m) and constituting part of the *Acropora-Millepora* subzone of the fore reef (Moreno et al. 1981). Surveys off Cozumel during 1984-86 characterized *A. palmata* as relatively common and noted its presence close to shore and on the tops of pinnacles on patch reefs found (Fenner 1988) contrary to the absence of dense stands (*A. cervicornis* or *A. palmata)* historically noted.

Belize

Studies at Carrie Bow Cay (Cairns 1982) noted that *A. palmata* was common in turbulent shallow waters, especially directly seaward and shoreward of the reef crest, but also in the shallow spur and groove zone (1 to 8 m depth). Additionally, because Belize is one of the few areas where multi-year quantitative data are available, those data are further analyzed and presented as a case study in section 4.5.3.

Honduras

Offshore of Honduras, *A. palmata* was characterized as intermediate (between rare and common) on fringing reefs of Roatan during the late 1980s (Fenner 1993). This species was also recorded from Cayos Cochinos, Bay Islands, during 1994-96 (Guzman 1998), and isolated colonies were found at 5 m depth on the windward sides of the islands (Ogden and Ogden 1998). Colonies were affected by the 1995-bleaching event in Cayos Cochinos (Guzman and Guevara 1998).

Nicaragua

Offshore (200 km east) of Nicaragua at Albuquerque and Courtown atolls, *A. palmata* was historically conspicuous on the lagoonal terrace from 0.5 to 3 m depth (Diaz et al. 1996). Sampling at Corn Island (eastern shelf of Nicaragua) during 1976-77 indicated *A. palmata* was the dominant frame-building coral on the reef crest, with isolated colonies on the fore reef slope (Roberts and Suhayda 1983). At the CARICOMP reef monitoring station at Great Corn Island, *A. palmata* was one of the dominant coral species; coverage was characterized as declining during the early 1990s, principally due to bleaching, pollution, and hurricane damage (Smith and Ogden 1994).

Costa Rica

Along the Caribbean coast of Costa Rica, *A. palmata* historically occurred on several reef complexes along the coast (Cortes and Guzman 1985a; b).

Panama

Distribution records for Panama include several sites along the Caribbean coast such as Galeta Reef (Porter 1972, Cubit and Williams 1983). This species historically dominated the reef flat (Porter 1972) and constructed the fringing reef at Galeta Point (Macintyre and Glynn 1976). Historically, *A. palmata* was present seaward of the breaker zone at Holandes Cay from 4 m to 6 m depth (Glynn 1973).

Columbia

Off the Caribbean coast of Colombia, distribution records for *A. palmata* include Erhardt and Werding (1975) and Ramirez et al. (1985). Areas of dead *A. palmata* were documented in Parque Nacional Los Corales del Rosario during 1983, with live cover only as high as 2% (Ramirez et al. 1985. *Acroprora palmata* was relatively rare in the Santa Marta area at 3 m depth and was not significantly affected by the 1987 Caribbean-wide bleaching event (Zea and Duque Tobon 1989). At Tesoro Island, Rosario Archipelago, *A. palmata* formed a reef framework on the fore reef terrace (2 to 9 m depth), but was dead by 1992 (Sanchez 1995). These data indicate that the mass mortality along the Caribbean coast of Colombia apparently occurred pre-1980. The CARICOMP reef monitoring station at Chenque Bay indicated that *A. palmata* was one of the dominant coral species in the early 1990s, but cover was declining principally due to disease, bleaching, and dynamite fishing (Smith and Ogden 1994).

Venezuela

Historically, *A. palmata* was historically considered rare off the Venezuelan coast presumably due to strong coastal upwelling. Surveys in the Golfo de Cariaco, northeastern coast of Venezuela, did not record *A. palmata* (Antonius 1980). Surveys at the CARICOMP reef monitoring station at Parque Nacional Morrocoy indicated that *A. palmata* cover was declining in the early 1990s, due principally to disease and bleaching (Smith and Ogden 1994). In the Netherlands Antilles (Islands of Aruba, Bonaire, Curacao), *A. palmata* was the primary constructor of the reef crest zone (Roos 1964, 1971). Surveys conducted around the Curaçao coastline indicated that *A. palmata* was absent from the inner bays (Roos 1971). Off Bonaire, where reefs are restricted primarily to the leeward coast by heavy surf conditions, shallow reefs were almost entirely built by *A. palmata* (Scatterday 1974). Northwest of Piscadera Bay, Curacao, Bak (1977) recorded 5% to 50% coverage in the 1970s with dense stands noted from 2 m to 4 m depth.

Further east along the coasts of Trinidad and Tobago, historical distribution records for *A. palmata* are rare. This coral was documented on reefs offshore of Trinidad, but was considered extremely rare from observations during the 1970s (Kenny 1988); the two recorded observations were on the north coast of the island. Apparently *A. palmata* has a restricted distribution in this area due to low salinity during the rainy season and sedimentation (high turbidity) associated with muddy, soft bottoms.

Further east along the South American coast, no distribution records for *A. palmata* exist (Leao 1986, Leao et al. 1988), with the genus *Acropora* notably absent south of the equator in the Atlantic region (Glynn 1973).

4.5.3 Case studies

The following are summaries of specific locations throughout the wider Caribbean where quantitative data exist illustrating the overall trends reported above; data are illustrated in Figure 7. It is important to note that the data are from the same geographic area, not repeated measures at an exact reef/site that would indicate more general trends. The overall regional trend depicted (Figure 7) is a >97% loss of coverage (area of substrate the species occupy). Additional qualitative data for many of the same locations is discussed in sections 4.5.1 and 4.5.2, and may not depict identical trends.

Florida Keys, FL

Several studies have been conducted since the 1970s in this region. At Carysfort Reef, a slight increase in coverage by *A. palmata* and 18% decrease in coverage of *A. cervicornis* between 1974 and 1982 was recorded (Dustan and Halas 1987). The *A. palmata* increase was accompanied by a decrease in mean colony size, indicating substantial fragmentation during the study period which the authors attribute largely to anthropogenic physical disturbance (boat groundings and visitor impacts). This suggests that any major white-band disease (WBD) impacts to *A. palmata* at Carysfort Reef probably occurred after 1982. However, the deeper reef terrace at Carysfort Reef, which was historically dominated by *A. cervicornis*, suffered dramatic loss of this species, probably due to disease that occurred before the reef was resurveyed in 1982. Between the summer of

1982 and April 1984, a complete loss of both species was reported at Carysfort (Szmant pers. comm.).

Jaap et al. (unpublished) characterized *A. palmata* populations at Elbow and French reefs as relatively stable from 1981-86. In contrast, disease and storms caused the demise of *A. cervicornis* at these reefs during the same period. Jaap et al. (1988) reported a drastic decline in *A. cervicornis* (96%) over the course of the same period, but stable *A. palmata* abundance at Molasses Reef. Jaap et al. (unpublished) also observed a complete loss of *A. cervicornis* at French Reef over the same time period, probably due to storms and/or disease. Again, this suggests that the major *A. palmata* decline, at least in the Key Largo area, took place after 1986.

A snapshot mapping study of Looe Key reef suggested areal (m^2) losses of ~93% and ~98% for *A. palmata* and *A. cervicornis*, respectively, between 1983 and 2000 (Miller et al. 2002a). Based on studies by Dustan and Halas (1987) and Jaap et al. (1988), it is quite likely that the 1983 baseline used in this study was already depressed, at least for *A. cervicornis*. A systematic survey of deeper reefs (13 to 19 m) along the entire Florida Reef Tract in 1995 found *A. cervicornis* to be present at only seven of 20 sites and never at more than 0.62% cover (Aronson and Murdoch, unpublished).

Data from a rapid assessment survey conducted throughout the Florida Keys from 1999 to 2001 reported mean coverage by *A. cervicornis* of 0.049% among eight habitat types surveyed (Miller et al. 2004). *Acropora palmata* mean coverage was even lower throughout the Florida Keys than its congener, even on many high-relief spur and groove reefs where it was formerly abundant. Among the eight habitat types surveyed, *A. palmata* was only recorded in high-relief spur and groove reefs where it was formerly abundant. Mean coverage in this habitat type was 0.158% and ranged from 0.158% in the lower Keys, 0.300% in the middle Keys, to 0.338% in the upper Keys.

A dramatic decline in *A. palmata* abundance was observed at 6 focal patches (including Carysfort, Molasses, and French reefs) in the Key Largo area since 1998 (mostly from 1998-1999) and little recovery since then (Miller et al. 2002b). This decline was most evident at sites where *A. palmata* occurs as sparse, individual colonies where total colony abundance fell by 77% between 1998 and 2001. This decline was less evident in denser thicket stands where mean colony density declined from 1.1 colonies/m_2 in 1998 to 0.8 colonies/m_2 in 2001.

The Florida Keys National Marine Sanctuary Coral Reef Monitoring Program (CRMP) documented that the percent cover contributed by *A. palmata* at Upper Keys reefs was low at the beginning of the study (7.2 to 7.3% in 1996) and declined to <1% by 2000. *Acropora cervicornis* coverage was even lower, declining during 1996 to 2000 from 0.13 to 0.03% in the Upper Keys. In 2003, where they occurred, average percent coverage was reported at 0.05% and 0.94% respectively, for *A. cervicornis* and *A. palmata* (CRMP unpubl. data).

More recent demographic monitoring (i.e., counting individual colonies rather than percent cover) of *A. palmata* in the Upper Keys indicates continued declines between 2004 and 2005. Of ~200 randomly selected *A. palmata* colonies located among five reefs, over 5% had died completely in nine months between March 2004 and January 2005 (Williams and Miller, unpubl. data). This rate of complete colony mortality was in addition to substantial partial mortality of other colonies in the sample population.

In comparison to the data reported above, Shinn et al. (2003) photo-documented decadal changes in *A. palmata* and *A. cervicornis* at Grecian Rocks and Carysfort Reef in the Florida Keys. At both sites luxuriant growth of these corals developed during the 1960s, flourished during the 1970s, but declined in the 1980s and showed no signs of recovery. Shinn's photo series starting in 1960 are available at http://coastal.er.usgs.gov/african_dust/gallery.html.

Dry Tortugas

The Dry Tortugas are located approximately 117 km west of Key West, Florida (24° 33' to 24° 44'N and 82° 46' to 82° 58'W). The area has an extensive history of research; for example, Alexander Agassiz (1882) published a map of the benthic marine communities in 1882. The Agassiz map reported the spatial coverage of the principal marine community components, including the spatial distribution of habitats dominated by *A. cervicornis* and *A. palmata* (Table 3).

Table 3. Terrestrial and marine habitats, Dry Tortugas, from Agassiz map (1882).

Habitat	Acres	Hectares	Percent
Land	108.7	44	0.20
Astrea and *Meandrina* Reefs	380.5	154	2.80
Staghorn reefs	**1030.4**	**417**	**1.90**
Elkhorn reefs	**108.7**	**44**	**0.20**
Broken coral heads	163.1	66	0.30
Total Coral Reef	1682.8	681	3.09
Octocoral-hardbottom	2607.0	1,055	4.80
Sediments	49,952.3	20,215	91.90
Total	54,350.8	21,995	

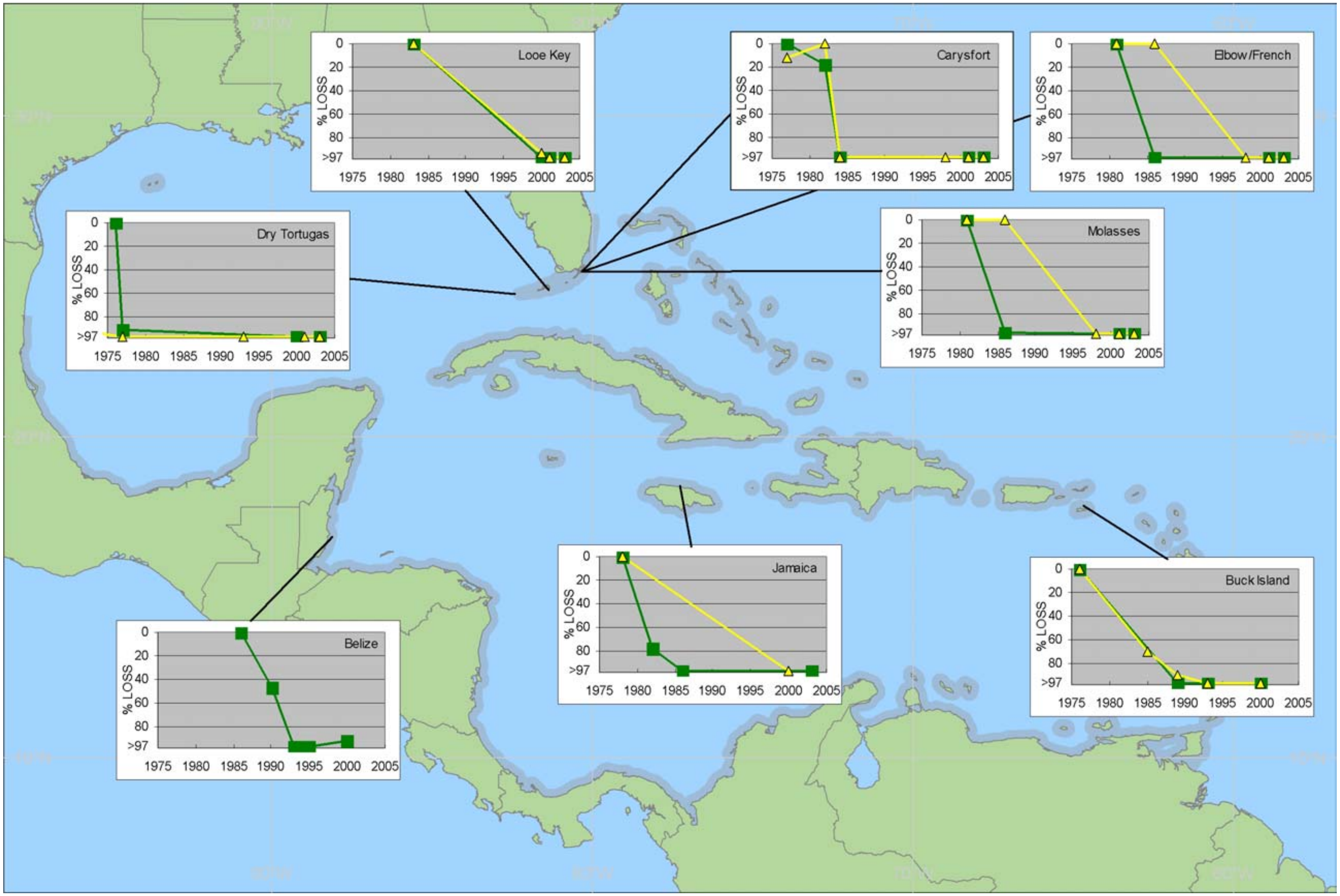


Figure 7. Percent loss of *Acropora cervicornis* (green squares) and *A. palmata* (yellow triangles) throughout the Caribbean for all locations (n=8) where quantitative trend data exist. Data sources are listed in text descriptions that follow.

These data are the earliest qualitative data for any western Atlantic reef system. The staghorn and elkhorn reefs contributed most of the reef habitat at Dry Tortugas shallow reefs. Unpublished field notes by John W. Wells of Carnegie Laboratory (1932) indicate that the occurrence of *A. palmata* reefs in the area during the early 1930s was similar to what Agassiz reported 50 years earlier. From the closing of the Carnegie laboratory in 1939 until 1973, there was a hiatus in reef research at Dry Tortugas. In 1982, Davis published a map of Dry Tortugas marine communities (Table 4).

Table 4. Terrestrial and marine habitats, Dry Tortugas, from Davis (1982).

Habitat	Acres	Hectares	Percent
Land	113.7	46	0.20
Bank Reefs	338.5	137	0.60
Coral head buttresses	620.2	251	1.10
Staghorn Reefs	**1181.2**	**478**	**2.10**
Elkhorn corals	**1.5**	**0.6**	**(.0026)**
Total Coral Reef	2140.7	867	3.8
Octocoral hardbottom	9,797.7	3,965	17.40
Benthic algae	281.7	114	0.50
Seagrasses	17,060.1	6,904	30.29
Sediments	26,914.7	10,892	47.80
Total	56,309.3	22,788	

Comparison of the Agassiz and Davis maps illustrated that the staghorn (*A. cervicornis*) reefs had increased slightly in area coverage, while the elkhorn reefs (*A. palmata*) virtually disappeared.

In January 1978, an extreme cold-water disturbance resulted in 95% or greater loss of *A. cervicornis* from the Dry Tortugas (Davis, 1982; Porter et al., 1982; Roberts et. al., 1982). Projects at Dry Tortugas have monitored coral abundance and cover at Bird Key Reef, west of Loggerhead Key (*A. cervicornis* thickets prior to the cold water disturbance), Pulaski Shoal, Texas Rock, and White Shoal. Neither *A. cervicornis* nor *A. palmata* populations have recovered (Jaap and Wheaton, 1995). Resurveys of these sites during 2002 and 2004 revealed some areas with a few colonies of *A. cervicornis*, but no general recovery (Jaap et al. 2002, in prep).

Jaap and Sargent (1993) published details on mapping of the *A. palmata* community in Five Foot Channel. They identified the community boundaries at 1,400 m^2, including both sparse and dense concentrations of *A. palmata*. The densest concentration of colonies, however, was confined to an area within 728 m^2, slightly larger than what Davis reported in 1982.

In 2002 Jaap and others in an expedition visited Five foot Channel and inspected the *A. palmata* and the *A. prolifera* communities. They had suffered from disease and/or environmental stresses. In 2000, a channel that separated Garden and Bush Keys filled in with sediment thus changing water circulation. The circulation at flood tide is from the southeast, through the Five Foot Channel gap, between Long Key and Bird Key Reef rampart. At ebb tide, the flow reveres and the source of water has changed; now water from and around the Garden Key anchorage (possibly including overflow from the Garden Key septic tank field) flows out Five Foot Channel (previously water from the channel between Garden and Bush Keys formed the principal volume).

In October 2004, an expedition visited the Five Foot Channel approximately a month after the eye of Hurricane Charlie passed over the Dry Tortugas (Jaap et al. pers. observ.). The storm apparently fragmented many corals and scattered these fragments as far inshore as within 100 m of the *A. palmata* and *A. prolifera* communities. Some fragments had healthy-looking tissue, and while the patches were reduced in upward relief, they did not seem to suffer catastrophic destruction. A site off the northeast side of Loggerhead Key (3 m deep) was also visited and was a site reported in 2002 to have a moderate population of *A. cervicornis* (Williams pers. comm.). Following the hurricane, this site experienced more severe disturbance: there were very few multi-branched colonies and most extant colonies consisted of small branch fragments. Many fragments had washed inshore (west) and ended up in a sparse *Thalassia* seagrass bed. The vitality of many fragments appeared satisfactory (color, few signs of disease and predation).

Overall throughout the long history of quantitative data across the Florida Keys reef system, a loss of greater than 97% coverage has occurred for each species (Figure 7).

Buck Island, U.S.V.I.

In 1976, five cross–reef transects were established at Buck Island, three on the northern coast (BI-3, BI-4, BI-5) and two (BI-1, BI-2) on the southern coast. At that time, the crest of the northern and southern bank-barrier reefs and the northern fore reef was composed of greater than 50% live *A. palmata*. *Acropora palmata* was the most abundant coral on the forereef slope down to the bank at a depth of 10 to 15 m in the northern and eastern sections of the reef. In the southern section, this species was dominant to depths of 3 to 4 m. *Acropora palmata* abundance was reported as 33% of total live coral cover. By 1984, when Anderson et al. (1986) surveyed the reef, the cover of *A. palmata* was dramatically reduced (approximately 70% loss) in the region of transect BI-3. Anderson et al. (1986) reported that most of the forereef had stands that were almost completely dead. Subsequently Bythell et al. (1989) surveyed the same transect and found that the *A. palmata* coverage had been reduced to 90% of 1976 abundances (Bythell 1989). Routine monitoring of these same transects was initiated in 1988. Through 2000, percent cover for *both A. cervicornis* and *A. palmata* continued to decline and no *Acropora* spp. were reported on the transects in 2000 (Bythell 2000). These data represent a >97% decline in cover of *Acropora* spp. in this area from 1976 through 2000 (Figure 7).

In the summer of 2004, 617 belt transects (each 250 m^2) were surveyed at Buck Island Reef National Monument (Mayor in prep.). *Acropora palmata* colonies were found in 74% of the transects (Figure 8). Extrapolating from these densities provides a rough estimate of about 100,000 large (over 1 m in greatest dimension) colonies within the entire hardbottom habitat (shallower than 10 m) around the island (783 ha).

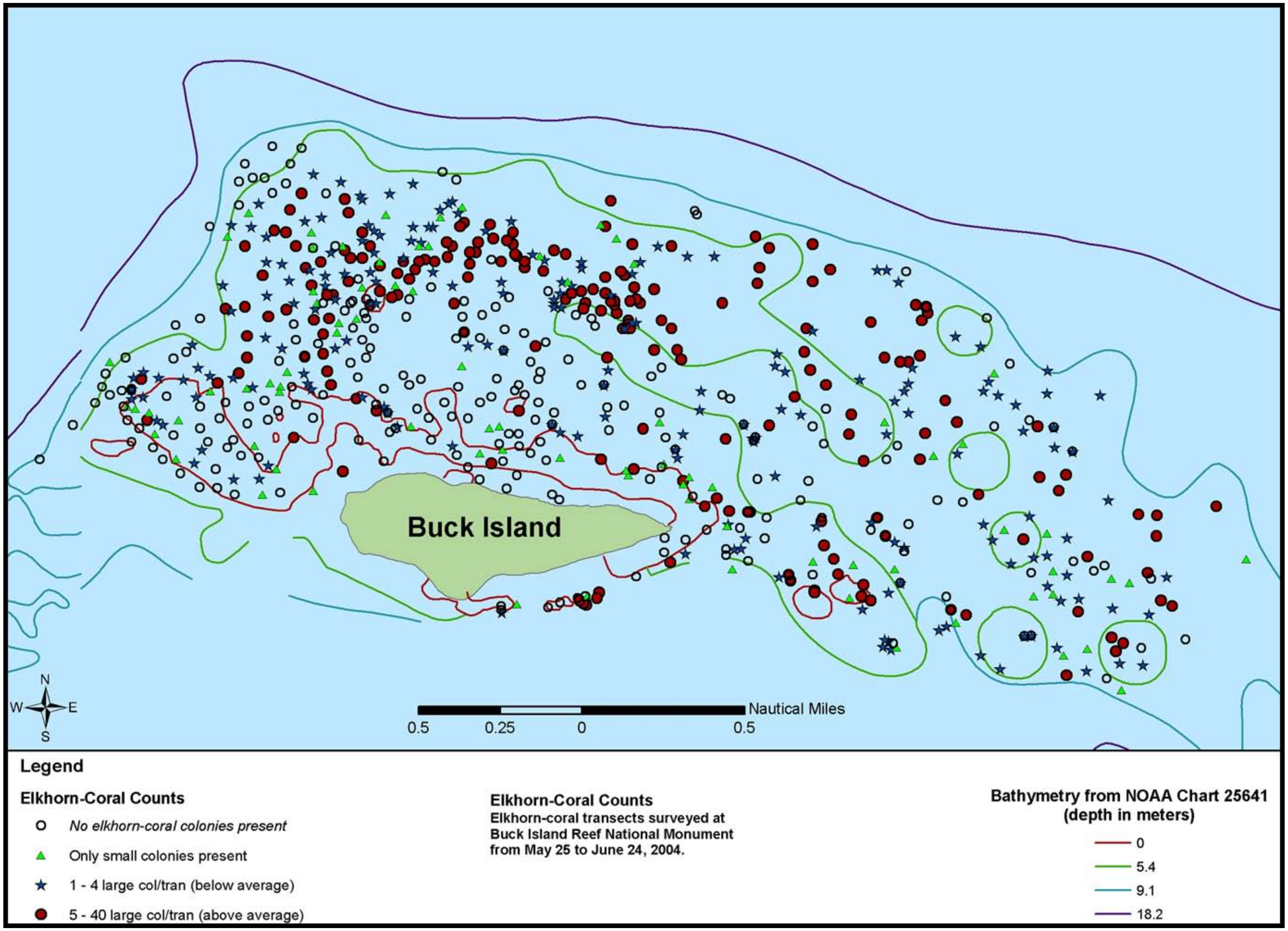


Figure 8. Location of *Acropora palmata* colonies as observed during a survey in summer 2004 at Buck Island Reef National Monument, U.S.V.I.. (Mayor in prep).

Belize

Both *A. cervicornis* and *A. palmata* were abundant along the Belize barrier reef and its atolls in the 1960s (Stoddart 1962). While extensive damage occurred in 1961 associated with Hurricane Hattie, with the exception of areas that received the most severe damage, substantial recovery occurred by 1972 (Stoddart 1974). Channel Cay in Belize was one of many sites that supported a healthy dense population with nearly 70% cover of live *A. cervicornis* in 1986 (Aronson and Precht 1997). By 1990 more than 25% of this population was affected by WBD, with subsequent declines in live cover to less than 40%. By 1993, the species was essentially gone from that site and there were no signs of recovery as of 1998 (Aronson and Precht 2001b). AGRRA surveyed several sites of similar habitat (coral ridge) and found *A. cervicornis* to represent 5% of live coral cover (Peckol et al. 2003), confirming that the temporal trend observed by Aronson and Precht (1997) was representative. Quantitative abundances for *A. palmata* are lacking in this area; however, like *A cervicornis*, this species is reported to be very abundant on the barrier reef and atolls during the 1960s (Stoddart 1962). AGRRA surveys in 1999 found that *A. palmata* represented less than 5% cover on the fore reef and patch reef habitats and found 'standing' dead colonies to be common at several sites (Peckol 2003). During the 1960s through 1997, there was a >97% loss of *Acropora* spp., with a slight increase in 1999 for a net loss of approximately 92% cover (Figure 7).

Jamaica

The original description of Caribbean reef zonation, including the zones named for *A. palmata* and *A. cervicornis* (Goreau 1959), was based principally on the reefs of the north coast of Jamaica, in particular Discovery Bay. Surveys in 1978 of the *A. cervicornis* zone estimated percent cover to be 51% in this area, specifically in the bay and on the west fore reef (Woodley et al. 1981, Tunnicliffe 1983, Wapnick et al. 2004). In 1980 Hurricane Allen passed by the north Coast and caused extensive damage to both *A. cervicornis* and *A. palmata* reducing coverage by 99 and 85%, respectively, resulting in the formation of a small chain of islets out of the *A. palmata* rubble (Gayle and Woodley 1998). Independent of the effects of Hurricane Allen, *A. cervicornis* inside the bay declined by 78% by 1982, presumably due to disease, as the branching framework was still intact. Marked colonies on the fore reef suffered 95% mortality between 1982 and 1986 (Knowlton et al. 1990). White-band disease was first observed on the fore reef in June 1980 (Woodley et al 1981) prior to the Caribbean-wide mortality of the long-spined sea urchin (*Diadema antillarum*) during 1983-1984. While current observations on *A. palmata* are lacking, prior to Hurricane Allen this species comprised from 78 to 97% of the coral cover on the reef crest (0.5 to 5 m depth) (Liddell and Ohlhorst 1987). As of 2000 the reef crest was characterized as '*palmata* rubble' (Gayle and Woodley 1998) suggesting that, like *A. cervicornis*, this species has not been able to recover. Since 1978 a >97% loss of *Acropora* spp. has occurred in Jamaica (Figure 7).

4.6 Long Term Change

The current decline of Atlantic *Acropora* spp. populations has been viewed as one of many insults to marine ecosystems caused by humans (Jackson 2001), but the detailed mechanisms of cause and effect continue to be elusive, in part because of a general lack of manipulative experiments testing various hypotheses (e. g., Miller et al. 1999). If similar population declines could be identified before significant human populations entered the Caribbean region, then it might be viewed that the present collapse is part of a natural cycle. However, conclusive paleontological evidence of mechanisms (e.g., fossil evidence of disease or bleaching) does not yet exist. Perhaps more promising are manipulative experiments to predict future responses of these corals to global changes. As specific forecasts of temperature, light, sea level, and carbon dioxide (CO_2) become more refined (Buddemeier et al. 2004), laboratory and field experiments should be able to better predict coral responses to changes in the global environment, although such approaches will not resolve other causes of mortality or changes in abundance and distribution.

4.6.1 The Geologic Record

Although Atlantic acroporids are known from the Early Miocene, about 15 million years ago (15 Ma), *A. palmata* and *A. cervicornis* appear to have developed during the late Pliocene (2-3 Ma) coincident with the closing of the Isthmus of Panama (NMITA 2004). These two corals were widely distributed throughout the Caribbean during the Pleistocene and Recent (1.8 Ma to present). Although the geologic record for *A. cervicornis* and *A. palmata* spans millions of years, it is by no means continuous and long gaps occur in their geologic record. These gaps may be viewed as occurring on three time scales that are a function of the elevation of fossil reefs (controlled by changing sea levels and sedimentation) and the ability to accurately date the time of coral growth. First, well-preserved corals that are many hundreds to thousands to millions of years old are dated using a combination of paleontological, geomagnetic, and radiometric methods. Second, corals a few hundred thousand years old are dated using radiometric methods alone. Third, on the time scale of 10 to 30 thousand years (10-30 ka), corals have typically been dated using radiocarbon. High-precision (mass spectrometric) methods of uranium-series dating have provided an order-of-magnitude more accuracy in dating and also allow the correction of radiocarbon dates for long-term variations of carbon-14 (^{14}C) in the atmosphere. *Acropora palmata* generally grows within 5 m of sea level and so is among the best, fossil sea-level indicators (Lighty et al. 1982). For this reason, geologists have taken special note of the occurrences of *A. palmata* in fossil reefs (Broecker et al. 1968, Greenstein and Pandolfi 1997). By comparison, little attention has been paid to the occurrences of *A. cervicornis* in the Pleistocene or Holocene. While *A. cervicornis* is often noted on species lists from fossil reef localities, it is not used for dating because its depth range is much greater than that of *A. palmata*. Fossil *A. cervicornis* thickets are known to occur in the Florida Keys and Bahamas and probably occur elsewhere, but have received little study. The hybrid *A. prolifera* is only known from modern examples.

Acropora palmata and *A. cervicornis* appeared during the late Neogene as part of an evolving community of Caribbean corals (Budd and Johnson 1999; Budd et al. 1999). Fossil records are known for 166 Caribbean coral species during the past 10 million years, and of these, 62% (103) originated during this period and 64% (107) became extinct. More than one third, 36% or 60 species, are alive today. Ninety-four of the 107 species (88%) that became extinct originated prior to 5 million years ago. Almost two-thirds of the corals that are alive today (37 species (62%)) originated during the past 5 million years, including *A. palmata* and *A. cervicornis*.

New dating information reported by Getty et al. (2001) suggests that an important locality in Costa Rica is considerably younger than previously thought. With this new dating information, it appears that the rate of extinction between 1 and 5 million years ago averaged about 10% of coral species per million years, but increased to 33% between 1 and 0.5 million years ago. Curiously, no corals are known to have gone extinct in the last 0.5 million years, perhaps an erroneous conclusion resulting from the inadequacy of the fossil record. Periods of high extinction are credited to changes in circulation and climate and not to specific impacts on corals.

4.6.1.1 Pleistocene Reefs

Our knowledge of Pleistocene corals comes from fossil reefs primarily formed during sea-level high stands that leave reef terraces along the margins of islands. Fossil reef terraces are known from Barbados as old as 450 ka (Mesolella et al. 1969). Particularly well-defined reefs are found during the time intervals 79-84 ka, 104-111 ka, 122-127 ka, 220 ka, and 260 ka. It is interesting to note that some of these terraces have a well-developed *A. palmata* zone, while others are described as having only a minimally developed *A. palmata* reef crest community. Based on growth rates of Holocene reefs, reef terraces represent only a few thousand years of growth, certainly less than 20 ka. Pandolfi and Jackson (2001) estimated that the top 2 m of the 125 ka reef at Curaçao was deposited in the range of 200 to 2,350 years. Thus, there are time gaps for tens of thousands of years, during which sea level was low, with no record of *Acropora* growth. Obviously the corals survived and presumably their fossil record could be found some 10s to 100s of meters below sea level. However, that information remains currently elusive. Geographically, the widest distribution of *Acropora* fossils is from the 125 ka sea-level high-stand. Fossil reefs of this age with *A. palmata* are known from Jamaica, Grand Cayman, Barbados, Haiti, the Dominican Republic, Puerto Rico, the Bahamas, Belize and Curaçao. Fossil reefs of this age without *A. palmata* (reported to date) occur in Florida, southern Cuba, Yucatan and Honduras.

Jackson (1992) pointed to repeated occurrences of acroporid corals in similar zones in fossil reefs as evidence of remarkable stability of reef ecosystems during the Late Pleistocene, a period of marked sea-level change. Pandolfi and Jackson (2001) and Hubbard et al. (2004) noted the similarity of abundance of *A. palmata* in ancient and pre-1980s Caribbean reefs. Pandolfi and Jackson (2001) interpreted the nonrandom distribution of coral species in space and time to indicate that the recent *Acropora* decline may be due to either unprecedented anthropogenic influences on reefs or fundamentally different patterns at varying spatio-temporal scales. One glaring exception to this similarity rule is the Key Largo Limestone, a well developed, 125 ka, fossil reef in the Florida Keys without an *A. palmata* reef crest (Hoffmeister and Multer 1968). In fact the Key Largo Limestone is apparently lacking any *A. palmata*, a phenomenon that obviously has nothing to do with human activity. The lack of *A. palmata* was recognized several decades ago and numerous hypotheses were put forward to explain this pattern (see Stanley 1966, Hoffmeister and Multer 1968). These hypothesis were most recently resurrected by Precht and Miller (in press) who exhaustively reviewed the current apparent anomaly and concluded that "when conditions have deteriorated, as in the Pleistocene, head corals have dominated and persisted" on the shallow-reef community in Florida. Precht and Miller (in press) apparently concur with the conclusions of Harrison and Coniglio (1985): the absence of *A. palmata* was the result of environmental stress. This explanation derives from the observations by Shinn et al. (1989) and Ginsburg and Shinn (1964, 1994) that describe Florida Keys reefs as stressed by shelf water from Florida Bay flowing between the Keys out to the reefs. During the growth of the Key Largo reef (~125,000 years ago) there was not an island barrier and the reef grew in water continually influenced by the Florida Shelf. This has been the accepted hypothesis since 1985 (Halley et al. 1997)

4.6.1.2 Holocene Reefs

Analyses of Holocene (and latest Pleistocene) fossil reefs lead to a somewhat different interpretation of the persistence of *A. palmata* stands. Several authors have recognized distinct breaks in the growth record of *A. palmata* during the past 15,000 years. Blanchon and Shaw (1995) determined three periods during which the reef-crest monospecific *A. palmata* zone was displaced by a deeper-water mixed species framework. These periods occurred at 14.2, 11.5, and 7.6 ka and appear to have been relatively short intervals (<1,000 years). The authors attribute these breaks to episodes of rapid sea-level rise that drowned existing reefs and led to the establishment of new reefs further inland.

Hubbard et al. (2004) identified two millennial-scale gaps in the *A. palmata* record at 3 and 6 ka. After considering a number of possible causes, they concluded that disease might be a possibility, largely based on elimination of other possible factors. They point to the lack of paleoecologic indicators for disease and recognize that a shallow-water Caribbean reef without *A. palmata* represents a temporal deviation from the norm. Although systematic study of fossil *A. cervicornis* has not occurred, Shinn et al. (2003) randomly selected and dated fossil *A. cervicornis* branches from a few centimeters below the sediment surface at 19 sites along the180 km-long Florida reef tract. They found two 500-year gaps in the abundance of this coral at ~4.5 ka and 3 ka and concluded that the documented decline in this coral during the past 25 years may not be without precedent in the Florida Keys. In contrast, Wapnick et al. (2004) found little evidence for a decline in *A. cervicornis* growth in Discovery Bay, Jamaica, during the past 1,000 years except for the current decline. They concluded that in the 1980s a combination of perturbations, including overfishing, caused an unprecedented disruption in the growth of *A. cervicornis*.

4.6.2 Projections of Global Climate Change

Buddemeier et al. (2004) reviewed possible consequences of global climate change (GCC) for coral reefs including potential changes in reef distributions. Although one might conclude that GCC would allow coral reefs to migrate to higher latitudes, Buddemeier et al. (2004) argued that migration is impeded because humans have altered the coastal areas where future reefs might form. Potential localities are unfavorable for reef development due to coastal development, overfishing, pollution, intensive agriculture and other human impacts. If global change results in a slowing of the oceanic thermohaline circulation, high latitude reefs that are sustained by northward flowing warm oceanic currents may be threatened. Other impacts from global change are increased temperature and bleaching, elevated CO_2 and reduced calcification, changes in the rate of sea-level rise, changes in ocean circulation, and changes in the frequency or intensity of storms.

4.6.2.1 Storm Impacts

Buddemeier et al. (2004) argue that there is little evidence for projected changes in storm frequency and there is no agreement on an increase of storm intensity with projected global climate change. However, there is general agreement that hurricane frequency has increased in the mid 1990s, after a 30-year lull in activity, back to levels experienced earlier in the 20th century. Goldenberg et al. (2001), in evaluating various studies comparing hurricane frequency changes and global climate change, stated that the data are as of yet inconclusive. Knutson et al. (2001, cited in the petition) produced models that indicated cyclones in the Pacific might increase in intensity by 5 to 12%. They noted that their study did not address the applicability of their results to other cyclone basins, such as the wider Caribbean. Similar uncertainty is expressed by Henderson-Sellers et al. (1998) who conclude that regional hurricane frequencies are not yet predictable. They also concluded that intensities will likely remain the same or increase at a modest 10 to 20%, changes that are and that these predicted changes are small compared with natural variations. Bengtsson at al. (1996) modeled the effects of greenhouse gas-induced warming and found that the frequency of storms would be significantly reduced. It seems safe to concur with Buddemeier et al. (2004) that there is no clear evidence for or against future changes in storm frequency associated with global climate change.

4.6.2.2 Temperature

Although most corals appear to be acclimatized to the long-term seasonal variation in temperature in their respective reef areas, an increase of only 1 to $2^{o}C$ above the normal seasonal maximum can induce bleaching (Fitt and Warner 1995). At any location, a bleaching threshold can be determined at a degree or two above the long-term seasonal maximum. It is well documented that the Earth's temperature has increased during the past century to levels that had not been reached in the previous 1,000 years. During the 20^{th} century, global average surface temperature increased by $0.6 \pm 0.2^{o}C$ (IPCC 2001). In particular, the decades of the 1980s and 1990s exhibited a rapid temperature rise to levels above the average for the previous millennia. Of course this average value is the mean of many local measurements, some of which are far more extreme than the average. The global trend is reflected in a number of long-term records of sea surface temperature (SST), but more importantly, the frequency of warm-season temperature extremes increased during the past two decades and is inducing more frequent episodes of coral bleaching. While coral bleaching patterns are complex, with several species exhibiting seasonal cycles in symbiotic dinoflagellate density (Fitt et al. 2000), there is general agreement that thermal stress leading to bleaching and mass mortality increased during the past 25 years (Brown 1997). In particular, during the years 1987, 1995, and 1998 widespread coral bleaching was witnessed throughout the Caribbean as a result of elevated SST (Williams and Bunkley-Williams 1990). Although there was some recovery from the 1987 bleaching event (Fitt et al. 1993) and the 1995 event, the 1998 bleaching resulted in high mortality rates at a number of Caribbean reef sites (Goreau et al. 2000).

Although *Acropora* spp. may be somewhat more resistant to bleaching than other stony corals, they are by no means immune. Most reports of the 1987 bleaching event noted that *A. palmata* and *A. cervicornis* retained normal colors while *Siderastrea siderea*, *Agaricia agaricites*, *Montastraea annularis*, *Porities porites*, and *Diploria strigosa* were severely bleached (Ogden and Wicklund 1988). Although much of the decline in abundance of these species took place before the severe bleaching episodes of the 1990s, bleaching of *A. palmata* was observed in 1998 at Looe Key, Coffins Patch, and Western Sambo Reefs in the Florida Keys (Causey pers. comm.) and at several sites in the upper Florida Keys where substantial mortality (largely partial mortality of colonies) ensued (Miller et al. 2002). Bleaching in *A. cervicornis* has rarely been described (Ghiold and Smith 1990, Williams and Bunkley-Williams 1990) and most of the documented loss during the past two decades is apparently due to disease (Peters 1984). However, bleaching is known to occur in both species and, when it persists for more than a few weeks, may cause mortality (Jaap 1979, Jaap 1985).

Using global climate models, predictions can be made about the future frequency of thermal events exceeding the bleaching threshold for a given area. Hoegh-Guldberg (1999) conducted this analysis for the south coast of Jamaica and found that a bleaching episode as severe as the 1998 event will become commonplace within 15 years and will occur annually in about 40 years. This assumes that the 1998 bleaching did not select for more temperature tolerant genotypes (see Baker et al. 2004)

Most of the coral bleaching literature recognizes temperature as a primary driver of bleaching, but it is also recognizes that other factors play important roles. Irradiance, particularly in the ultraviolet (UV) range (Gleason and Wellington 1993), is perhaps as important as temperature and may be a limiting factor in the dispersal of coral larvae (Wellington and Fitt 2003). There is also indication that elevated CO_2 (Pêcheux 2002) can lead to bleaching. Microbial infection was observed to cause bleaching during warm seasons in *Oculina patagonica*, a Mediterranean coral (Kushmaro et al. 1996, Kushmaro et al. 1997). UV irradiance may be a limiting factor in dispersal of larvae from corals (Wellington and Fitt 2003).

Buddemeier and Fautin (1993) proposed that bleaching may be an adaptive mechanism that allows corals to acquire more thermally tolerant symbionts. The evidence for adaptation was reviewed by Coles and Brown (2003) who stated that the variability in bleaching response was not taken into account by previous modeling efforts. Baker et al. (2004) documented thermally tolerant symbionts becoming more abundant on reefs that have recently bleached. They conclude that bleaching may lead to reefs that are more resistant to future thermal stress, "resulting in significantly longer extinction times for surviving corals". Increased seawater temperature may also have synergistic effects, causing pathogens to grow faster and be more virulent. These effects are discussed more fully in section 6.3.

4.6.2.3 Sea level

Rapid rises in sea level can affect *A. palmata* by both submerging it below its common depth range and by degrading water quality through coastal erosion or enlargement of lagoons and shelf areas. *Acropora cervicornis* is only affected by the latter, given its much greater depth range compared to *A. palmata* and the hybrid, *A. prolifera*.

Blanchon and Shaw (1995) argued that a sustained sea-level rise of more than 14 mm/yr will displace *A. palmata* from its framework range (0 to 5 m) into its remaining habitat range (5 to 10 m) where a mixed framework is likely to develop. Sea-level change is unlikely to lead to extinction in the next several hundred years by this process because sea level is not predicted to rise that rapidly in the near future (Church and Gregory 2001).

Both *A. palmata* and *A. cervicornis*, however, will be affected by decreased water quality as a result of shoreline erosion and flooding of shallow banks and lagoons. The threat of these processes can be assessed on a site-by-site basis using criteria such as the geological character of the shoreline and topography. Where topography is low and/or shoreline sediments are easily eroded, corals may be stressed by degrading water quality as sea-level rise proceeds. Flooded shelves and banks at higher latitudes (greater than 15° N) may alter the temperature or salinity of seawater to extremes that can then impact corals during offshore flows. This process has been termed reefs that "are shot in the back by their own lagoons" by Neumann and Macintyre (1985). Although this process could be widespread, there will be many areas, particularly on the windward side of rocky islands, where erosion and lagoon formation will be minimal.

4.6.2.4 Carbon Dioxide

Atmospheric carbon dioxide has increased from about 280 parts per million (ppm) in the early 1800s to current levels of about 380 ppm (Prentice 2001). As atmospheric CO_2 is dissolved in surface seawater, seawater becomes more acidic shifting the balance of inorganic carbon species away from CO_2 and carbonate (CO_3^{-2}) toward bicarbonate (HCO_3^{-1}). This shift decreases the ability of corals to calcify because corals are thought to use CO_3^{-2} as the source of carbonate to build their aragonite ($CaCO_3$) skeletons. Numerous laboratory experiments and experiments in Biosphere 2 have shown a relationship between elevated CO_2 and decreased calcification rates in corals and other $CaCO_3$ secreting organisms (Reibesell et al. 2000, Barker and Elderfield 2002). Kleypas et al. (1999) calculated that coral calcification could be reduced by 30% in the tropics by the middle of the 21st century. Corals grown during laboratory experiments that doubled atmospheric CO_2 manifested a 11 to 37% reduction in calcification (Gattuso et al. 1999, Langdon 2003, Marubini et al. 2003).

It is interesting to note that a few studies of the historic growth rates of corals during the last century concluded that some corals are calcifying more, not less, despite changes in atmospheric carbon dioxide levels (Lough and Barnes 2000, Bessat and Buiges 2001). The corals examined in these studies responded positively to increased temperature, thus negating any decrease due to elevated CO_2.

5 Existing Regulatory Mechanisms

In order to assess the adequacy of current management measures (i.e., the fourth ESA listing factor) that could prevent further decline of *A. palmata* and *A. cervicornis*, the BRT researched and summarized, by authority, existing regulatory mechanisms that afford protection to corals. In most cases, management actions were aimed at protecting coral or coral reefs in general and did not specifically mention *Acropora* spp. A brief assessment of management measures within the U.S. and foreign jurisdictions follows with each regulation further detailed in Appendix A. The adequacy of these mechanisms is addresses in section 6.2.

5.1 Federal

Existing federal regulatory mechanisms and conservation initiatives most beneficial to branching corals have focused on addressing physical impacts, including damage from fishing gear, anchoring, and vessel groundings. Depending on the specifics of zoning plans and regulations, marine protected areas (MPAs) can help prevent damage from collection, fishing gear, groundings and anchoring. Because all corals, particularly branching growth forms such as *Acropora* spp., are susceptible to such impacts, MPAs can afford some immediate protection from this type of damage. Regarding the effectiveness of MPAs, enforcement capacity generally is lacking in the wider Caribbean, thus compromises a central function of zoning plans. Many federal resource managers, for example, emphasize the need for strengthening enforcement capacity. When they are effective, no-take MPAs prohibit all collection of marine life and other resources, with the goals of protecting biodiversity and sensitive habitats, and restoring ecosystem processes. These types of broad protections actions are likely to benefit *Acropora* populations. 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 *Acropora* spp.

Both the *A. palmata* and *A. cervicornis* corals are included on NOAA's candidate species list (see section 2.1.1). While species on this list do not receive any protection under the ESA; their inclusion is designed primarily to highlight species at risk and to seek additional data regarding distribution and abundance.

Included in Appendix A are details about Fishery Management Councils and Fisheries Management Plans; Executive Orders and Acts of Congress; and National Parks, Monuments, Reserves, and Marine Sanctuaries.

5.2 State/Local

Florida statutes and rules protect all of the Scleractinia and Milleporina corals from collection, commercial exploitation, and injury/destruction on the sea floor (FS 253.001, 253.04, Chapter 68B-42.008 and 68B-42.009). Additionally, Florida has a comprehensive state regulatory program that regulates most land, including upland, wetland, and surface water alterations throughout the state. The comprehensive nature of the state program is broader than the federal program in that it also regulates alterations of uplands that may affect surface water flows. This regulatory program also includes a Federal-State Programmatic General Permit and implementation of a state-wide National Pollutant Discharge Elimination System (NPDES) program. In addition, activities located on or using State-owned sovereign submerged lands also require applicable proprietary authorizations, including consent agreements, leases, and easements.

In Puerto Rico there exist several laws and proposed regulations 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. These zones will facilitate the Department of Natural Resources (DNER) in controlling human activity, such as anchoring, that can directly impact *Acropora* spp. Law 147 also directs the DNER to identify and mitigate threats to coral reefs from degraded water quality due to pollution and additionally directs the DNER to designate priority areas as marine reserves, including a minimum of 3% of the insular platform within three years (2003). Marine reserves are defined as areas where all extractive activities are prohibited in order to help recover depleted fishery resources and protect biodiversity, and can protect *Acropora* by preventing impacts from fishery gear. There are currently an additional 13 natural reserves in Puerto Rico that have coral reefs within their boundaries, all of which are located on all coasts and offshore islands. This spatial distribution of protected areas provides an infrastructure for management measures to protect *Acropora* spp. populations.

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 within their boundaries (including *Acropora* spp.) and encompass 7% of the shelf around St. Croix, and 3% of the St. John/St. Thomas shelf. Most recently (2002) the Virgin Islands Legislature passed Bill 12 that approved the establishment of additional large marine park on the eastern end of St. Croix (St. Croix East End Marine Park).

5.3 International

There is considerable variation in relevant management actions throughout the nations within the Caribbean region. While many Caribbean nations have enacted some sort of coral conservation program/regulation, most proactive coral initiatives/efforts in the region are small-scale with, at best, localized effects. Appendix A summarizes relevant regional programs and agreements by nation; it is important to note that many of these efforts are ongoing at specific locations and are thus not being implemented nation-wide.

6 Analysis of Listing Factors

A species may be listed under the ESA if it is threatened or endangered because of any of the following five 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.

Because coastal marine ecosystems are complex and subject to a myriad of threats that potentially impact *Acropora* spp., the BRT elected to categorize these threats according to their level of impact as either *sources*, *stressors*, or *responses*. Sources are natural or anthropogenic processes that create stressful conditions for organisms (e.g., climate change or coastal development). A stressor is the specific condition that causes stress to the organisms (e.g., elevated temperature or sediment runoff), while the response of the organisms to that stressor is often in the form of altered physiological processes (e.g., bleaching, reduced fecundity or growth) or mortality. Thus, threats via habitat alteration (i.e., ESA listing factor A) can be comprised of both sources and stressors. Once stressors and sources were identified, the BRT then tabulated and classified each stressor into one, or more, of four (factor A, B, C, and E) ESA listing factors (Table 5). Section 6.1 further discusses sources, stressors and responses for *Acropora* spp. A few of the threats described in the listing petition were not deemed by the BRT to represent relevant impacts to the Atlantic *Acropora* spp. Specifically, in terms of coral disease, shut-down reaction is not discussed because there is no clear indication in the literature that it is a disease affecting in situ *Acropora* spp. populations. Similarly, competition with other corals (e.g., *Agaricia* or *Porites*) is not deemed to be a threat to *Acropora* spp. colonies given that the instances of "replacement" cited in the petition followed *Acropora* spp. mortality events. Finally, because *Acropora* spp. are not known to grow under overhangs, the BRT determined that trapped exhaust air from divers was not a threat to Atlantic *Acropora* spp. The remaining ESA listing factor (inadequacy of existing regulatory mechanisms) is analyzed in section 6.2 and summarized in Table 8. It is important to note that all of these threats to Atlantic *Acropora* spp. are occurring against a backdrop of radical ecosystem change that has occurred on most Caribbean coral reefs during at least the past two decades.

Table 5. Association of identified stressors to *Acropora palmata and A. cervicornis*, Endangered Species Act (ESA) listing factors, and Federal and State Regulations that may alleviate threats by ESA factor. Additional information for each Federal and State regulation is provided in Appendix A. Possible source(s) for each stressor are listed below each stressor, but these lists are not exhaustive. ESA Listing factors are:

A = the 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 = the inadequacy of existing regulatory mechanisms
E = other natural or manmade factors affecting its continued existence

Stressor	**ESA Factor**	**Federal and State Regulations**
Natural Abrasion and breakage Sources: storm events	A	Executive Order 13089, Continental Shelf Act, Coral Reef Conservation Act of 2000, Magnusen-Stevens Act, Coastal Zone Management Act 0f 1972, The Rivers and Harbors Act of 1899, The Clean Water Act of 1987, National Parks, Reserves and Sanctuaries, FKNMS Act of 1990, FL statute 253.04, 68B-42.009, Outstanding Florida waters, ERP, Submerged Lands, NPDES, SPGP, FL Clean Vessel Act, Laws of Florida Chapter 99-395, Phosphate Ban, PR Law 147, MPA
Sedimentation Sources: land development/run-off dredging/disposal sea level rise major storm events	A	See above
Anthropogenic Abrasion and breakage Sources: divers vessel groundings[1] anchor impact[2] fishing debris	A&B	See above for "A", plus Coral Reef Conservation Act of 2000, Coastal Zone Management Act 0f 1972, National Parks, Reserves and Sanctuaries, FKNMS Act of 1990, FL statute 68B-42.009,MPA
Temperature Sources: hypothermal events global climate change power plant effluents ENSO events	A&E	See above for "A" plus Continental Shelf Act, Coral Reef Conservation Act of 2000, Magnusen-Stevens Act, Coastal Zone Management Act 0f 1972, The Rivers and Harbors Act of 1899, The Clean Water Act of 1987, National Parks, Reserves and Sanctuaries, FKNMS Act of 1990, FL statute 253.001, 253.04, Outstanding Florida waters, ERP, Submerged Lands, SPGS, Phosphate ban, PR Law 147, MPA
Competition Source: overfishing	A&E	See above

Nutrients Sources: point-source non-point source	A&E	See above
Sea level rise Source: global climate change	A&E	See above
Over-harvest Source: aquarium/curio demand	B	See above
Disease Source: undetermined/understudied	C	None identified
Predation Sources: overfishing natural trophic reef interactions	C	See above
Contaminants Sources: point source non-point source	E	See above
Loss of genetic diversity Source: population decline/bottleneck	E	See above
African Dust Source: desertification	E	See above
CO_2 Source: fossil fuel consumption	E	See above
Sponge boring Source: undetermined/understudied	E	See above

[1] resulting from operator error due to harbor management

[2] resulting from operator error due to lack of alternatives

6.1 Summary of Stressors

Disease

Coral diseases have had severe effects on Caribbean coral reefs in general and *Acropora* spp. populations in particular. Evidence exists demonstrating 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 agent of the region-wide decline of Atlantic *Acropora* spp. beginning in the late 1970s. White band disease (WBD) is generally attributed with the majority of disease-related mortality in both *A. cervicornis* and *A. palmata* (Aronson and Precht 2001). However, as with most coral diseases, the inconsistent phenomenological description of *Acropora* spp. disease mortality patterns, and the lack of identification of a specific pathogen has greatly hindered the ecological, let alone epidemiological understanding of WBD impacts and, more importantly, control. More recently, a second disease termed white pox (WPx) has been described as having drastic impacts on *A. palmata*, and a specific pathogen has been identified as the cause (Patterson et al. 2002).

White band disease (Photos 18a-b) was originally described in *A. palmata* 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 wide that grades proximally into algal successional stages” (Gladfelter 1982). Reported rates of advance on *A. palmata* average 5.5 mm/day (Gladfelter 1982). Specific literature descriptions of WBD in *A. cervicornis* 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). There is little information on the rate or pattern of progression. Aronson and Precht (2001) suggest that WBD has had greater impact on *A. cervicornis* than *A. palmata* population decline, perhaps due to differential susceptibility. However, it is probable that the term WBD has been applied to a range of conditions, particularly in *A. cervicornis* where the round branching colony morphology constrains the manifestation of mortality patterns (i.e., whatever kills *A. cervicornis* generally must sweep up or down a branch). 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, 1997).

Ritchie and Smith (1995, 1998) described a disease in *A. cervicornis* 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*. This etiology is under active investigation (Weil and Smith pers. comm.).

Photo 18. White band disease on *Acropora palmata* in (a) Florida Keys and (b) Buck Island, U.S.V.I. Photo credit M. Miller (a) and P. Mayor (b).

The other major disease affecting *A. palmata* is known by the name white pox (WPx) (Photo 19a-b, 20a). The bacterial pathogen, *Serratia marcescens*, has been demonstrated via Koch's postulates to cause WPx. White pox is "characterized by the presence of irregularly shaped white lesions where tissue has disappeared from the skeleton. Lesions range in area from a few square centimeters to greater than 80 cm^2 and can develop simultaneously on all surfaces of the coral colony" (Patterson et al. 2002). Significant mortality of *A. palmata* (up to 85% of still living colonies killed in certain sites) in the Florida Keys within the past 8 years has been attributed to WPx (Patterson et al. 2002). However, the reliance on phenomenological field identification of disease indications makes it implausible to attribute all irregular white lesions on *A. palmata* to this pathogen. Subsequently, other researchers have used the more general term "patchy necrosis" to refer to irregular denuded skeleton lesions affecting *A. palmata* (e.g., Bruckner and Bruckner, 1997, Rodriguez-Martinez et al. 2001); this term will be used interchangeably in the following discussion. It is likely that some, but not all lesions described as patchy necrosis in the literature are indeed attributable to *Serratia marcescens*. Although most *Acropora* spp. decline in the 1970s to 1990s is attributed to WBD, the incidence of WPx appears to be increasing and most monitoring information after 2000 indicates that WPx has higher prevalence in *A. palmata* than WBD (see below).

In *A. palmata*, the prevalence of WPx can vary substantially even over a small geographic area (USGS unpublished data, Weil et al. 2002, pers. comm.). 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% of the colonies on six reefs were affected by an outbreak in 2000, many of the colonies recovered completely.

Although WPx has been described as a "new" disease (Patterson et al. 2002), there are early descriptions in the literature that are consistent with WPx. Bak and Criens (1982) described an outbreak of "virulent" disease on *A. palmata* (and *A. cervicornis*) 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. Within two weeks, the damage reached a maximum number of about 50 dead spots per ($9m^2$) quadrat" (Bak and Criens 1982)). Rogers et al. (2005) also document WPx-like lesions on *A. palmata* from Buck Island, U.S.V.I., in 1970 (022b).

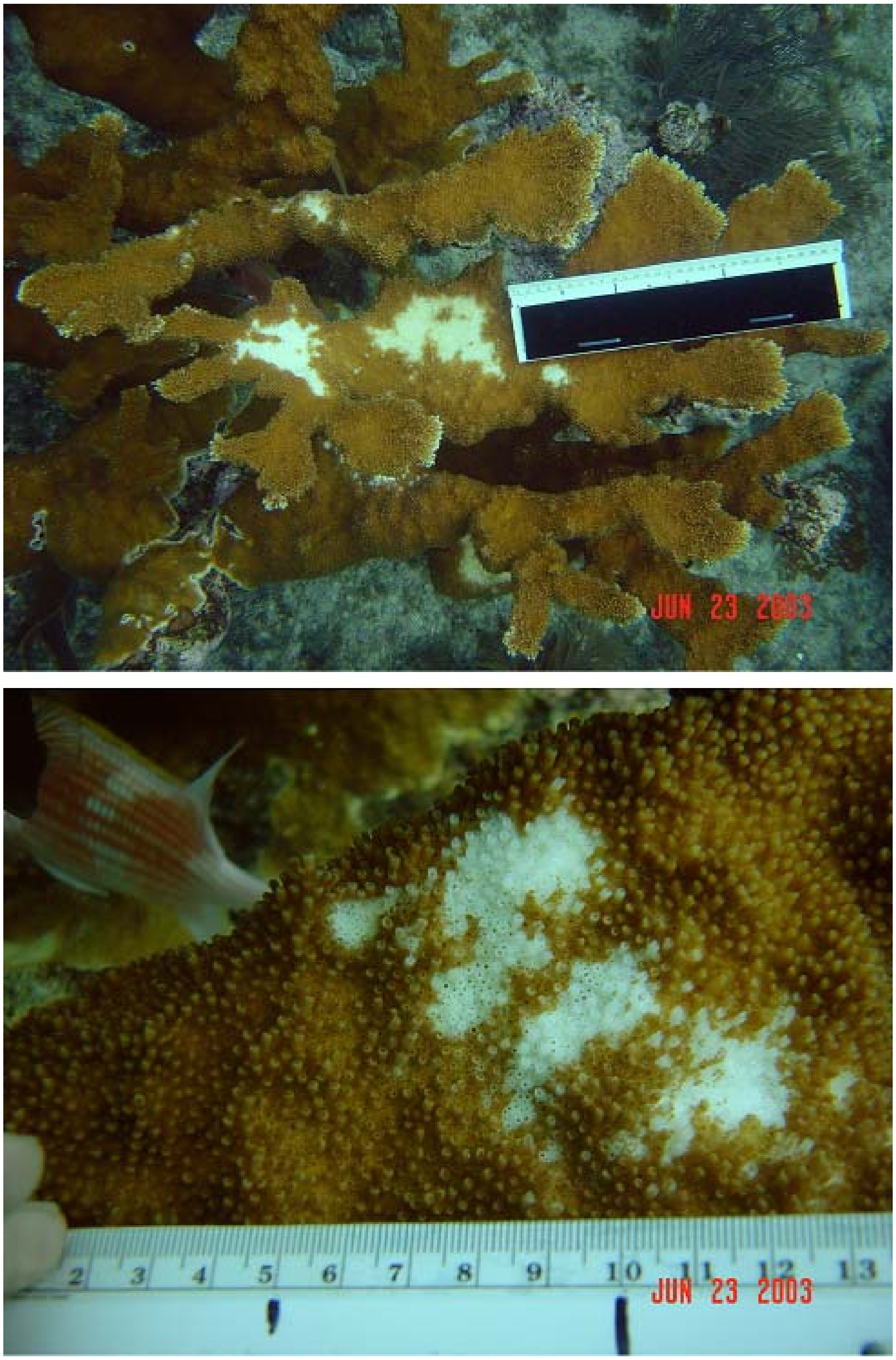


Photo 19. Two examples of white pox disease on *Acropora palmata*, Florida Keys. Photo credit M. Miller

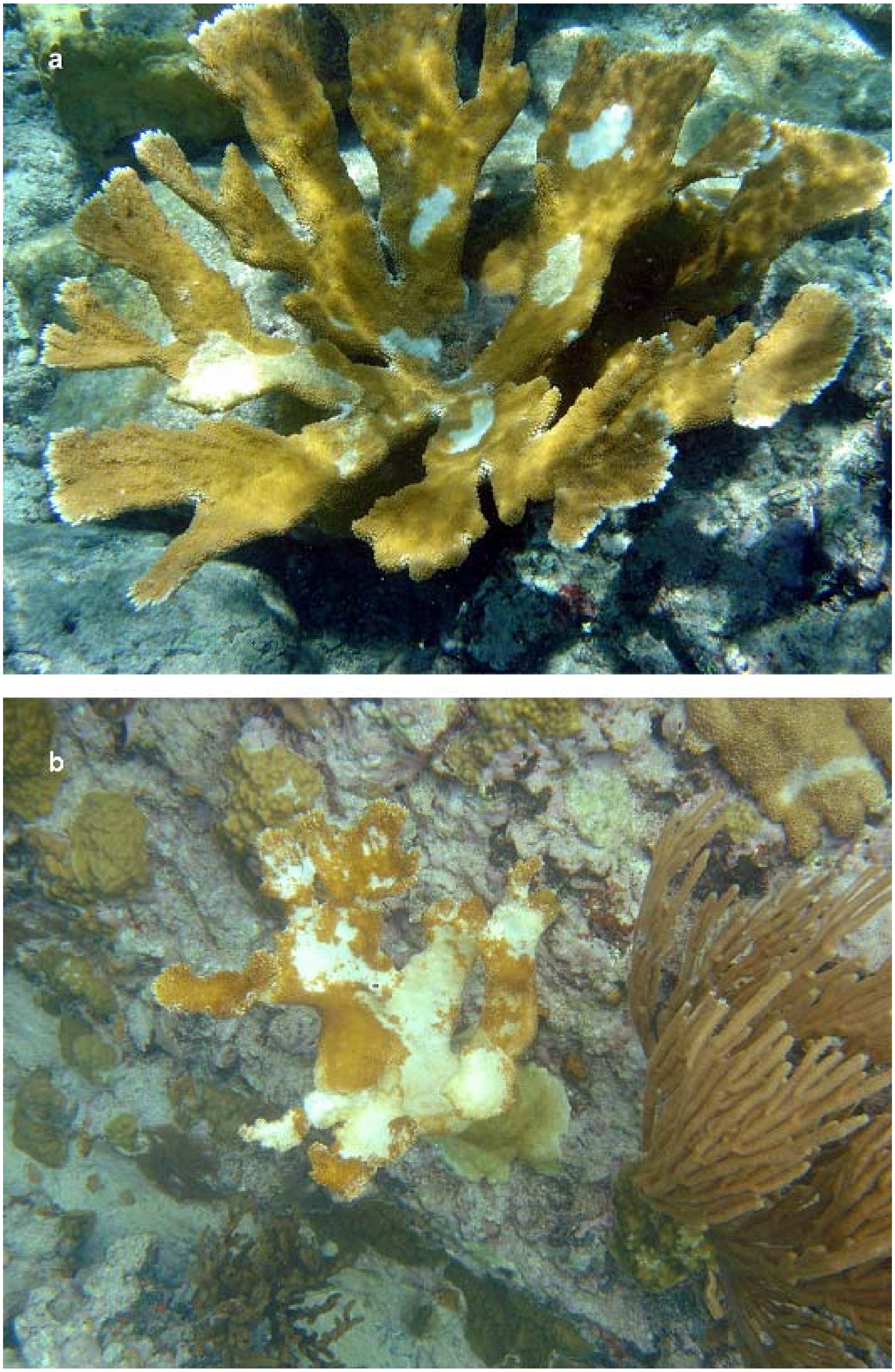


Photo 20. Examples of two diseases [white pox (a) and unidentified (b)] on *Acropora palmata*, St. John, U.S.V.I. Photo credit C. Rogers.

Diseases continue to have a devastating impact on existing *Acropora* spp. populations. For example, an outbreak in the Florida Keys in 2003 affected 72% of tagged colonies of *A. cervicornis* (n=20) involved in a recovery monitoring project, with 28% of these suffering complete mortality and many more colonies ending up as tiny remnants of live tissue (<10% of colony alive; Williams and Miller, in review). Mean rates of colony tissue loss were variable, but generally very rapid, averaging ~ 13 cm^2 tissue per day, but ranging up to 42 cm^2 per day (Williams and Miller in review). During this same time period, an *A. prolifera* patch in Dry Tortugas National Park also suffered a disease outbreak, but prevalence and mortality were not quantified. In contrast, ongoing monitoring of extensive *A. cervicornis* thickets to the north in Broward County, Florida, did not detect disease during this same period (B. Vargas-Angel pers. comm.)

Disease status/prevalence in baseline conditions is available from various targeted monitoring programs. During the summer of 2004 at Buck Island Reef National Monument, diseases were recorded on *A. palmata* colonies in 42% of the transects, WBD was found in 11%, and WPx in 37% of the transects (Mayor in prep.). At 10 reefs around the island of St. John surveyed between August and November 2004, the percentage of *A. palmata* colonies with WPx varied from 2 to 34%. Meanwhile, only a single colony with WBD appeared in a recent St. John survey (Rogers and Muller unpub. data). Targeted annual monitoring of *A. palmata* at six reefs in the upper Florida Keys from 1997 to 2003 indicated a mean disease prevalence (WBD and WPx combined) ranging from 2 to 9% (n=6 reefs), but outbreak conditions of WPx were observed at one of these sites in 2004 (Miller and Williams unpub. data). Notably, no similar estimates are available from targeted monitoring of *A. cervicornis* in these areas (U.S.V.I. and Florida Keys); because its density is so much lower than *A. palmata*, this has hampered monitoring efforts due to widely scattered colonies.

Florida Keys surveys at 204 sites during 1999 through 2001, representing a range of hard-bottom and coral reef habitats, were sampled for disease prevalence affecting *Acropora* spp. (Swanson et al. in review). Approximately 7.7% (±5.9% SE) of *A. palmata* sampled from northern Key Largo to south of Key West were recorded having dead white skeleton of unknown cause(s), while another 5.5% (±5.5% SE) were documented with WBD. Over the same study area, 0.4% (±0.4% SE) of *A. cervicornis* colonies were recorded as having dead white skeleton of unknown cause(s) and none were noted with active WBD conditions.

The Atlantic and Gulf Rapid Reef Assessment (AGRRA) surveys, conducted from 1997 to 2000, provide a valuable regional overview. However, the data on *Acropora* diseases must be viewed with some caution because of the difficulty of identifying the different diseases in the field and the varying expertise and experience of the observers (Lang 2003, P. Kramer pers. comm.). 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, cumulating 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. Also, repeated observations in specific sites over time (e.g., upper Florida Keys, USVI, Puerto Rico) suggest that the incidence of patchy necrosis has been increasing over time.

In the 1997-2000 AGRRA surveys, the most frequently observed disease condition in *A. palmata* was patchy necrosis, while WBD was more prevalent in *A. cervicornis*. Over 4% of *A. palmata* colonies were affected by disease, with higher disease prevalence in the Netherlands Antilles (north) (18%), Bahamas (12%), Cayman Islands (7%), and Turks and Caicos (6%). Five areas had no signs of disease on *A. palmata*, specifically Costa Rica, Netherlands Antilles (south), Panama, U.S.V.I., and Venezuela. At least 6% of *A. cervicornis* colonies were diseased, with greater prevalence documented from the Turks and Caicos (21%) and Cayman Island (20%), while U.S.V.I. (13%), Cuba (8%), and Bahamas (6%) had higher than average levels. Areas where no disease was recorded on *A. cervicornis* were Jamaica, Mexico, Netherlands Antilles, Panama, and Venezuela. Low to moderate disease prevalence was documented along most of Cuba's south coast, but 38% of the *Acropora* at one site were affected. Both WBD and patchy necrosis were more prevalent during summer months and there was a strong correlation between disease and recent mortality at the surveyed sites. Recent mortality was higher during 1998 and part of 1999, and was attributed to temperature stress during the 1998-99 El Niño-La Niña event.

While overall (e.g., Western Atlantic-wide) disease prevalence of 4 to 6% as indicated by the AGRRA data may not appear to constitute a significant threat, it should be noted that this is an instantaneous measure and thus gives no indication of the rapidity with which mortality might result.

Because of the lack of understanding of basic etiology, very little is known regarding the root causes of coral diseases. The decadal scale temporal coincidence of increased disease impacts with increasing anthropogenic pressures to reef systems suggests that a link may exist, though Aronson and Precht (2001) note that there were no obvious spatial patterns of WBD impact and human population pressures during the major early 1980s WBD epizootic. That is, WBD devastated *Acropora* spp. populations both near and far from intense human habitation (see, for example Curran et al. 1994). However, current monitoring surveys in St. John U.S.V.I. show higher prevalence of WPx lesions on *A. palmata* at sites with less coastal development/human population (Rogers and Muller unpub. data). The discovery of *Serratia marcescens* as a causal agent of WPx is suggestive of an anthropogenic source, as this bacterium is a human enteric resident and raises the possibility of a direct linkage with human sewage pollution. As there are a myriad of possible sources of this bacterium (i.e., it can occupy a variety of animal guts, as well as varied environmental conditions), more careful field microbiology work is needed to explore this possibility. More recently, Bruno et al. (2003) showed that experimental nutrient enrichment in the field approximately doubled the extent of tissue loss of so-called yellow band blotch disease, a condition that affects massive mounding corals (primarily *Montastraea* spp.), but not *Acropora* spp. 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). Increased numbers of *A. palmata* colonies with WPx 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, Rogers et al. Figure 10).

Growth anomalies, characterized by protuberant whitened masses of tissue and skeleton that overgrow normal polyps, have been observed on *A. palmata* colonies off the Florida Keys and Netherland Antilles and to a much lesser extent in *A. cervicornis* in the Caribbean (Peters et al. 1986). These lesions result in slow tissue loss, reduced branch extension, and loss of reproductive potential. Referred to as calicoblastic epitheliomas, these rare lesions do not appear to be caused by an infectious agent, but more study is needed.

Although the number or identity of specific disease conditions affecting Atlantic *Acropora* spp. 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 *A. palmata* and *A. cervicornis*. 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.

Temperature

Corals thrive in seawater temperatures between 25 and 29°C (Wells 1956, 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. August and September are the warmest months of the year (mean seawater temperature ranges from 27.7 to 31.4°C, Florida reef lighthouse data 1879-1899, Vaughan 1918). Mayer (1914) reported that the lethal temperature for *A. palmata* was between 34 and 35°C. Shinn (1966) reported that *A. cervicornis* expelled zooxanthellae at or near 33°C. High temperature results in physiological stress responses. Heat shock proteins are detectable with biomarker techniques. Pentoxides and other physiological products result in changing the intracellular environment driving the zooxanthellae to leave or decompose (bleaching).

Bleaching (zooxanthellae loss) can affect coral growth, maintenance, reproduction and survival. In contrast to statements in Jaap (1979) that bleaching at that time was thought to be of minor consequence (low morbidity and mortality), mass bleaching events have occurred in the 1980s and 1990s in all of the tropical ocean basins. In several cases there have been severe mortality and local extirpations of certain coral species. The bleaching events have become more frequent, are spatially more widespread, and the impacts are more intense during the past quarter century (Douglas 2003). This pattern of increasing frequency and intensity of bleaching impacts on coral reefs throughout the world is projected to continue (Hoegh-Guldberg 1999). Global climate change is raising global atmospheric air and sea temperatures, and shallow reef habitats are especially vulnerable.

Over-harvest

Corals are not consumed as food, thus the exploitation is not classic fishery stock management (maximum sustainable yield, etc). However, there is continued demand for corals to use in aquaria or for decorative purposes. In fact, the U.S. imports 80% of the global trade in corals and it is probable that collection would pose a serious threat to *Acropora* in the absence of existing regulations. Commercial coral collecting has been banned in State of Florida waters since 1974 (Jaap 1984) and was extended to U.S. territorial waters in the Gulf of Mexico and U.S. South Atlantic. Historically, shell and curio shops sold colonies of *A. palmata* and *A. cervicornis*, but usually claimed that specimens were collected in Haiti (Porter 1987).

In the Florida Keys during the early 1960s, major concerns over coral and fish collection, as well as treasure salvage, led to a campaign to protect resources off of Key Largo and resulted in the establishment of John Pennekamp Coral Reef State Park, the first of its kind in the U.S. The park eliminated fish traps and coral collection in 1960, although line fishing and commercial lobster trapping continued. By 1975, an estimated 400,000 people/year were paying admission to the park. Coral reef vitality surveys conducted in 1974-75 suggested physical and chemical impacts (Dustan 1977, Dustan and Halas 1987), but the main impacts to reefs were from snorkelers, divers, anchoring, and small vessel groundings.

Natural Abrasion and Breakage

Hurricanes cause more physical damage to acroporids than any other source. While the thick fronds of *A. palmata* and the interlocking branching morphology confer some degree of protection from storms that *A. cervicornis* does not have (Tunnicliffe 1981, Rogers et al. 1982), such storms can lead to the complete destruction and mortality of entire reef zones dominated by these species. These major storms have physically disrupted reefs throughout the wider Caribbean (Photo 21) and are among the primary causes of *Acropora* spp. loss in certain locations (Woodley et al. 1981, Rogers et al. 1982, Lirman and Fong 1997). For example, the effects of Hurricane Allen (1980) on the north coast of Jamaica included extensive mortality of both *A. cervicornis* (98% mortality) and *A. palmata* (95%) on shallow (< 10 m) reefs (Porter et al. 1981). Well after the storm struck the north coast, mortality of storm-generated fragments (especially *A. cervicornis*) continued, principally due to predation by snails and sea urchins (Knowlton et al. 1981). However, in some instances, corals are able to recover from such disturbances, as was documented in repeated photographs at Grecian Rocks, Key Largo (Shinn 1976, 1989). In the Florida Keys, hurricanes struck the area about once every seven years until 1965. If most offshore reefs began to form at about 6,000 ka, then reefs in the Florida Keys have been impacted to one degree or another by hurricanes ~800 times since their formation (Shinn 1989).

The last seven years have had the highest number of hurricanes on record and the 2004 hurricane season is one of the worst. Storms in 2004 smashed *A. palmata* and *A. cervicornis* colonies throughout a large portion of their ranges in the U.S.V.I., Turks and Caicos, Barbados, and Florida. Assessment of the damage is still underway. Although considered to be a means of asexual reproduction, fragmentation is only successful under suitable circumstances (Shinn 1976). For example, water quality must be sufficient to support the organisms, predation pressure needs to be low, and fragments need to be dispersed in favorable habitats (Tunnicliffe 1981, Bowden-Kerby 2001b). As stated previously in this document, while there is general agreement that hurricanes have increased in frequency over the last decade there is no clear evidence for or against future changes in storm frequency associated with GCC (Buddemeier et al. 2004). Interestingly, there is some evidence to suggest that the luxuriant coral growth observed on many Caribbean reefs during the 1950s and 1960s may have been due a lower frequency of hurricanes relative to the longer-term Holocene average (Shinn 1976).

Anthropogenic Abrasion and Breakage

Human activity in coral reef areas is another source of abrasion and breakage of *A. palmata* and *A. cervicornis*. These activities include boating (Photo 22), anchoring, fishing, recreational SCUBA diving and snorkeling, and an increasing variety of maritime construction and development activities. The shallow habitat requirements of *A. palmata* in particularly, render it susceptible to damage from such activities.

Divers and snorkelers

Given the aesthetic attractiveness of the Atlantic *Acropora* spp., corals and associated species, they are engaging to recreational sightseers using either snorkel or SCUBA. As with so many human impacts to corals, the effects of recreational divers are difficult to quantify and are clearly dose-dependent. Novice snorkelers/divers may stand on or kick *Acropora* spp. causing breakage, although there are no studies that document the frequency of this damage. A study by Talge (1990) systematically observed recreational divers in the Florida Keys. Divers with gloves were reported to have significantly higher numbers of interactions with all types of corals than divers without gloves. Males had more interactions than females, and SCUBA divers had more interactions than snorkelers (Talge 1990). However, the study showed that weekly touching had no detectable level of impact to the corals (Talge 1991). The Cayman Islands Department of the Environment (CIDE) studied diver impact at mooring buoy sites off of Grand Cayman Island. They concluded that sites with visitation greater than 5,000 divers per year (14 divers a day) resulted in coral injuries, while sites that had 15,000 divers in a year experienced a major loss in coral diversity and cover. Figure 9, from the Cayman Island report, illustrates a strong negative correlation between the number of annual person-dives at a certain dive site and the perceived quality of that site. This suggests that heavy usage by recreational divers/snorkelers may degrade coral reefs, and that limiting diver usage may enhance reef condition. For example, although diver impacts have not been evaluated, coral reefs and artificial reefs in the Florida Keys support 3.6-million person-days of snorkeling and SCUBA diving by residents and visitors (Table 6) per year. It is plausible that this level of usage is having ecological impact on Florida Keys coral reefs including its remnant *Acropora* spp. populations.

Photo 21. Storm damaged *Acropora palmata*, St. John, U.S.V.I. Photo credit C. Rogers.

Photo 22. Boat damaged *Acropora palmata*, St. John, U.S.V.I. Photo credit C. Rogers.

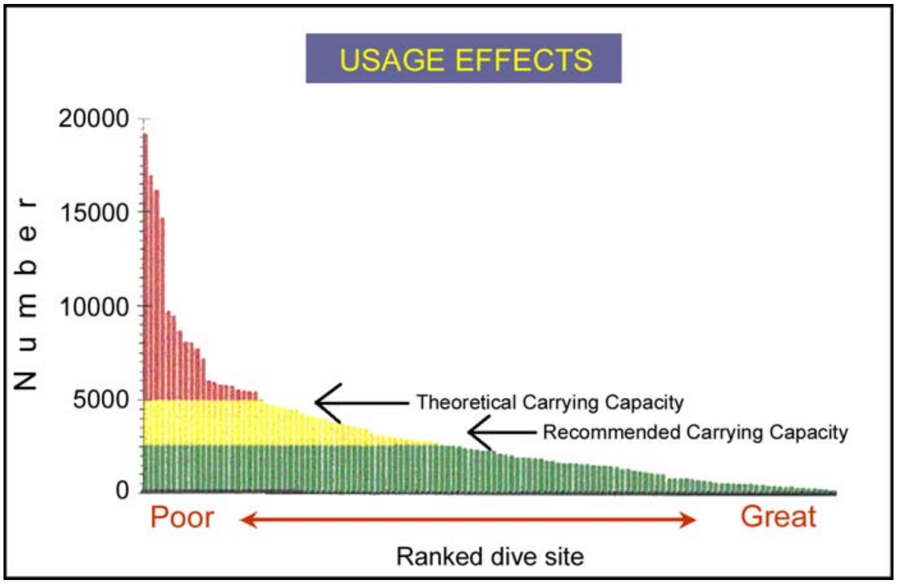


Figure 9. The total number of dives per moored dive site around Grand Cayman in 1994 (Cayman Islands Department of the Environment).

Although mooring buoys are typically thought to reduce boat impacts on reefs, limited studies that looked at mooring buoys and usage (numbers of divers per mooring/year), report that mooring concentrated injuries due to diver/snorkeler interactions, particularly to the fragile and rare corals close to the mooring (CIDE 1994).

Table 6. Number of person-days (millions) spent using reefs in the Florida Keys, June 2000 to May 2001 (Johns et al. 2001).

Activity	Residents	Visitors	Total
Snorkeling	0.99	0.76	1.75
Scuba Diving	1.57	0.36	1.93
Fishing	0.48	0.88	1.36
Glass-bottom Boat	---	0.075	0.075
Total	**3.04**	**2.08**	**5.11**

Vessel groundings due to operator error/harbor management

Ship groundings on coral reefs have occurred ever since humans first built boats and began going to sea. Modern steel ships pose a much greater threat to coral reefs than wooden sailing ships. A modern large steel ship is a powerful mass and its impact can dislodge and fracture corals, pulverize coral skeletons into small debris-rubble, displace sediment deposits, flatten the topography, and destroy or fracture the reef platform. Salvage operations often result in additional damage due to inappropriate methods and poor control of operations. In some cases, the ship's hull is ruptured, and cargo and fuel are spilled on the reef.

Large ship groundings cause fundamental changes to a reef's structural topography and biological communities. For example, the *Columbus Iselin* foundered in the spur and groove habitat at Looe Key Reef after the 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 *Acropora* spp., where the ship came to ground and, since the ship was hard aground for several days, the pounding of the hull on the reef resulted in structural injuries to the reef foundation. Large ship groundings off the southeast Florida coast occurred from 1973-2004 and have degraded significant reef habitat (Table 7).

Table 7. Summary of large ship groundings off southeast Florida, 1973-2004.

Region	Number of groundings	Habitat area injured (m^2)
Palm Beach, Broward, Miami-Dade Counties	9	21,008
Monroe County	14	14,597
Dry Tortugas	5	17,836
Total	28	53,441

The shallow habitat of *A. palmata* 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. For example, in the last two years, two boats have grounded on *A. palmata* reefs inside Virgin Islands National Park, St. John. In April 2002 an 85-foot ferry boat struck Johnson's Reef, damaging approximately 3700 m^2 of coral reef. It was calculated that approximately 920 m^2 of coral was injured or destroyed, mostly *A. palmata*. In August 2002, another vessel (a 60-foot sportfishing boat) struck Johnson's Reef from the other side, damaging approximately 1650 m^2 of coral reef. Thirty-five corals, mostly *A. palmata*, were injured or destroyed. Similarly, multiple groundings have affected *A. palmata* at Western Sambo reef in the Florida Keys in the recent past. While approximately 60 to 90 small vessel (vessels less than 30 m) groundings on coral reefs are reported annually to the State of Florida (Fish and Wildlife Law Enforcement records), it is likely two to three times that number go unreported. These smaller-scale groundings damage individual colonies and are less likely to impact the framework or topography of the reef.

Anchor impact due to operator error/lack of alternatives

Anchor (and chain) damages occur in many areas. The size of the anchor, weather, and frequency of anchoring are directly related to the magnitude of the damages. In most areas with high tourist visitation, chronic anchor damage to coral reefs has been mitigated by installing special mooring buoys that eliminate the need to anchor (Halas 1985, 1997; see section 8). Fishing fleets that anchor in the same area for relief from adverse weather can also cause major damage (Davis 1977). In areas where large ships anchor on coral reefs, the damage can be significant; especially if the area is a designated anchorage or is frequently visited by large ships. 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, thus resulting in dislodged and fractured corals for hundreds of meters (Smith 1988).

Fishing debris and damaging fishing practices

Fishing is the most widespread exploitative activity on coral reefs and poses significant threats to the biodiversity and condition of marine ecosystems (Jennings and Polunin 1996). Marine fishery resources on a global scale are under intensive pressure from fishing (Botsford et al. 1997), and from the perspectives of fisheries managers, environmentalists and scientists, there is general agreement that habitat degradation is the most important threat to the long-term recovery of exploitable fisheries stocks (Benaka 1999). Fishing can influence the population structure of species by affecting their abundance, size, growth and mortality, but can also modify species interactions such as competition and predation by altering structural complexity (Russ 1991, Auster and Langton 1999). Various ecological effects occur when traps and bottom trawls are deployed, but impacts may also occur when large numbers of anglers use hook-and-line gear to fish (Jennings and Lock 1996, Jones and Syms 1998). Derelict fishing gear can destroy benthic organisms and entangle both benthic and mobile fauna, (Donohue et al. 2001), especially *Acropora* spp., due to their branching morphology.

Trawling and other types of fishing gear can be harmful to coral reefs. Trawls can dislodge and abrade corals, and stationary gear such as traps can damage branching corals by breaking branches off as they move across the sea floor or by directly landing on them. This is particularly true in the case of storms that can mobilize traps and often snare buoy lines in branching corals such as *Acropora*. In deep-reef habitats, trawling has devastated coral communities off Alaska (Krieger 2001), Ireland (Wheeler et al. 2003), and Norway (Hovland et al. 2001). In Alaska the principal corals were octocorals and in the North Sea the injuries were to *Lophelia pertusa*. Fishers in some parts of the world employ explosives or toxic chemicals such as sodium hypochlorite and sodium cyanide to harvest fish and invertebrates (Campbell 1977, Alcala and Gomez 1987, Eldredge 1987) and although no specific studies have been conducted on *Acropora* spp., these practices are expected to be detrimental.

In a recent study (2001) of 63 offshore coral reef and hard-bottom sites in the Florida Keys, Chiappone et al. (2005) quantified the impacts of lost fishing gear to coral reef sessile invertebrates. Lost hook-and-line fishing gear accounted for 87% of all debris (N=298 incidences) encountered and was responsible for 84% of the 321 documented impacts to sponges and benthic cnidarians, predominantly consisting of tissue abrasion causing partial individual or colony mortality. Branching gorgonians (Octocorallia) were the most frequently affected (56%), followed by milleporid hydrocorals (19%) and sponges (13%). Because *Acropora* spp. were relatively rare, few impacts from lost fishing gear were noted for these species. In general, the factors affecting the impacts of lost fishing gear include sessile invertebrate density, the density of lost fishing gear, and gear length. While lost hook-and-line fishing gear is ubiquitous in the Florida Keys, it was estimated that <0.2% of the available milleporid hydrocorals, stony corals, and gorgonians in the habitats studied were adversely affected in terms of colony abrasions and partial mortality.

Competition

Coral reefs are described as space-limited systems and thus it is believed that competition for space is an important structuring factor. Because of their fast growth rates and canopy-forming morphology, *A. palmata* and *A. cervicornis* are known to be competitive dominants within coral communities, in terms of their ability to overgrow other stony and soft corals (Photos 23-24). However, other types of reef benthic organisms (i.e., algae) have higher growth rates and, hence, expected greater competitive ability than *Acropora* spp. Since the 1980s, many Caribbean reef areas have undergone a shift in benthic community structure involving reduced cover by stony corals and increased coverage by macroalgae. This shift is generally attributed to the greater persistence of macroalgae under reduced grazing regimes due to human overexploitation of herbivorous fishes (Hughes 1994) and the regional mass mortality of the long-spined sea urchin in 1983-84. Impacts to water quality (principally nutrient input) are also believed to enhance macroalgal productivity.

Aronson and Precht (2001) emphasize, however, that these Caribbean-wide changes in benthic assemblages were precipitated by massive coral mortality events (namely the loss of *Acropora* spp. from WBD) as macroalgae are generally unable to actively overgrow and kill live corals. In other words, the coral-dominated Caribbean reef system was resistant to reduced herbivory regimes for a period of time as long as corals maintained their occupation of space. However, when coral mortality occurred, macroalgae were able to pre-empt that space (especially following the loss of grazing by *Diadema*) and were subsequently resistant to coral re-colonization (Hughes and Connell 1999). Thus the described shifts have been persistent on a decadal scale. The noted exception is in areas where the grazing sea urchins (*Diadema antillarum*) have recently recovered and removed the macroalgal dominants, thereby clearing space to allow enhanced coral recruitment (Edmunds and Carpenter 2001).

In summary, macroalgae are now the major space-occupiers on many Caribbean reefs. Their dominant occupation of reef surfaces impedes the recruitment of new corals (McCook et al. 2001) and hence, recovery by sexual recruits of *Acropora* spp. It is unlikely, however, that macroalgae have major impacts as direct competitors with healthy adult colonies. Other encrusting invertebrates may also pose a direct overgrowth threat to small colonies or bases of *Acropora* spp., but the extent of such interactions is not well documented.

Photo 23. *Acropora palmata* overgrowing a hard coral of *Diploria* spp. at Navassa. Photo credit M. Miller.

Predation

Acropora spp. are subject to invertebrate (e.g., polychaete, mollusk, echinoderm) and vertebrate (fish) predation, but “plagues” of coral predators such as the Indo-Pacific crown-of-thorns outbreaks (*Acanthaster planci*) have not been described in the Atlantic. Predation may directly cause mortality or injuries that lead to invasion of other biota (e.g., algae, boring sponges).

Photo 24. ***Acropora palmata*** **overgrowing** ***Gorgonia ventalina*** **at Navassa. Photo credit M. Miller.**

The most important predators on Atlantic *Acropora* spp. are the fireworm, *Hermodice carunculata*, and the muricid snail, *Coralliophila abbreviata*. Both these predators will feed on a wide range of cnidarian prey, but may prefer *Acropora* spp. *Hermodice* are commonly found enveloping the long branch tips of *A. cervicornis* (Photo 25) that are subsequently left devoid of tissue (Marsden 1962, Lizama and Blanquet 1975, Dustan 1977). *Hermodice* also feeds on branch tips or protuberances of *A. palmata*, where the predation scars appear as white patches (Porter 1987). Vargas-Angel et al. (2003) report a density between 86 and ~618 *Hermodice* ha^{-1} in *A. cervicornis* thickets in southeast Florida with predation scars affecting <0.2% of the *A. cervicornis* cover. There are few other data on the prevalence or impact of *Hermodice* on *Acropora* spp. populations. Although these predators rarely kill entire colonies, there are several possible mechanisms of indirect impact. Because they prey on the growing tips (including the apical polyps), especially of *A. cervicornis*, growth of the colony may be arrested for prolonged periods of time. Additionally, *Hermodice carunculata* from the Mediterranean Sea has been shown to serve as a vector for a bacterial bleaching pathogen in laboratory experiments (Sussman et al. 2003).

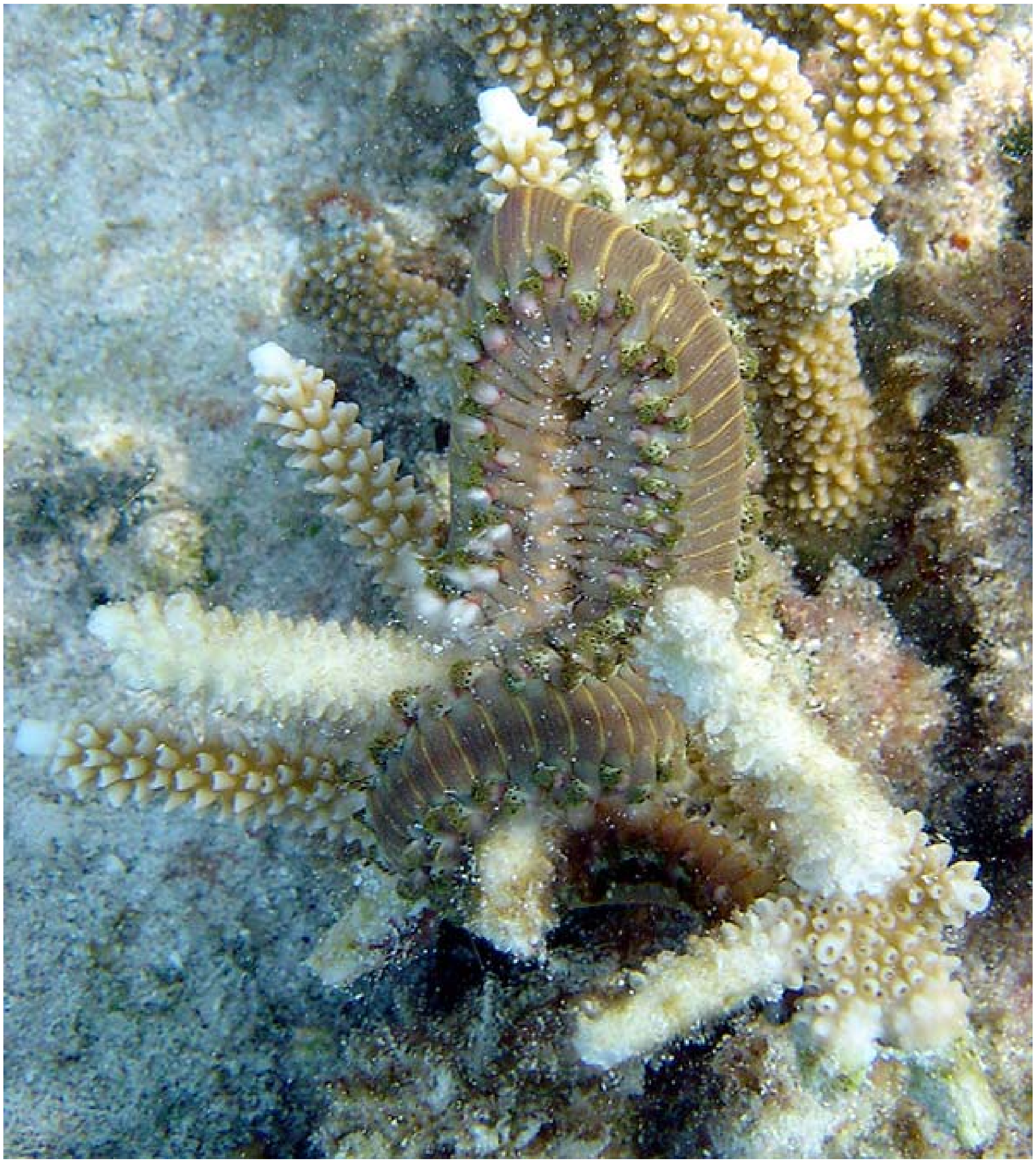


Photo 25. *Hermodice sp*. feeding on *Acropora cervicornis*. Photo credit D. Williams.

The other important predator of Atlantic *Acropora* spp. is the gastropod, *Coralliophila abbreviata* (Photo 26). This predator also feeds on a wide range of corals, but seems to be particularly damaging to *Acropora* spp. (Baums et al. 2003b). Prevalence data from throughout the Caribbean indicates that approximately 10 to 20% of *Acropora* spp. colonies harbor snails (Baums et al. 2003a). The rate of consumption by *Coralliophila* is highly variable, but may reach 6.5 cm^2 of coral tissue per snail per day (Bruckner et al. 1997) and probably averages ~1.5 cm^2 of coral tissue per snail per day (Baums et al. 2003b). Given that the mean snail density on infested *A. palmata* colonies is reported at over three snails per colony (Bruckner et al. 1997, Baums et al. 2003a) with a maximum of at least 23 snails per colony (Baums et al. 2003a), snail predation clearly represents a significant potential source of tissue loss. There is evidence that these predators concentrate on remnant *Acropora* populations following host coral decline (Knowlton et al. 1990, Baums et al. 2003a). For example, after Hurricane Allen struck the north coast of Jamaica in 1980 and greatly reduced the acroporid population, *C. abbreviata* continued to feed on remnant *A. cervicornis* colonies, reducing the population further (Knowlton et al. 1981). It should be noted, however, that *Coralliophila* seem to be extremely rare or absent on *Acropora* spp. in certain areas (e.g., Bocas del Toro, Panama, Baums pers. comm.; Dry Tortugas, Miller pers. observ.).

Photo 26. *Coralliophila abbreviata* feeding on *Acropora palmata*. Photo credit M. Miller.

The three-spot damselfish (*Pomacentrus planifrons*) and other species in the genus establish algal nursery gardens within branching *Acropora* spp. when available and on other coral species when acroporids are rare (Thresher 1976, Brawley and Adey 1977, Kaufman 1977, Itzkowitz 1978, Williams 1978, Sammarco and Carleton 1982). Although not predators in the strict sense, the damselfishes nip off living coral tissue, thus denuding the skeleton to make a place for their algal gardens. Again, it is likely that *P. planifrons* impacts are proportionally greater when the abundance of *Acropora* is reduced. Observations in several areas (e.g., Dry Tortugas, Navassa) suggest that isolated small colonies, particularly of *A. cervicornis*, have a very high prevalence of damselfish occupation (Photo 27).

Photo 27. Three-Spot Damselfish resident in isolated *Acropora cervicornis* colony in St. John, U.S.V.I. Greenish algal turf area in center right of photo was actively killed by the damselfish. Also note active disease (white lesions) in lower left portion of the colony. Photo credit: D. Williams.

Other predators also consume *Acropora* tissue to a lesser degree. Although not widely documented, the Caribbean long-spined sea urchin (*Diadema antillarum*) is known to feed upon live *Acropora* coral tissue (Bak and van Eys 1975, Sammarco 1980). Laboratory experiments confirmed that this sea urchin will feed on coral tissue when starved, but may also do so when feeding on turf algae when sea urchin population numbers are relatively high (e.g., >4 individuals/m^2) (Porter 1987). More recent studies indicate that besides damselfishes, parrotfishes, such as the stoplight parrotfish (*Sparisoma viride*), may also incidentally feed upon *Acropora* tissue. Very little is known concerning the extent of parrotfish grazing on Atlantic *Acropora* spp., but monitoring in the Florida Keys indicates that these scars usually heal in a matter of weeks to months (Williams pers. comm.).

Overall, predators can have important direct and indirect impacts on *A. palmata* and *A. cervicornis*. Predation impacts are greater in the current scenario of low coral abundance as coral predators have not been subject to the same degrees of disturbance mortality and their broad diet breadth has allowed them to persist at high levels despite decreases in acroporid prey. However, predation impacts on *Acropora* spp. appear to be much lower in certain geographic areas.

Sedimentation

Scleractinian corals are sessile, light-dependent animals that cannot move away from stressful situations (Marshall and Orr 1931; Cortes 1985; Rogers 1990). Early reports noted that shallow-water, tropical reef corals require highly transparent, sediment-free water (Wells 1957, Stoddart 1969). Other studies indicated that some corals can tolerate episodic turbidity (Hubbard and Pocock 1972) and, in some settings, chronic sediment loading. There is clear variation among coral species in the mechanisms and degree of sediment tolerance. The ability to remove sediments from the colony surface is an important behavioral characteristic influencing the growth, survival, and distribution of corals such as Atlantic *Acropora* spp. Corals reject sediment from their tissues using gravity, beating cilia, and trapping the sediment in their mucus and discarding the sheet of mucus/sediment. For example, *Manicina areolata* (rose coral) has the ability to use hydraulic pressure (filling the gastrovacular cavity with water and expelling the water in a pulse) to rid tissues of sediment. *Montastraea cavernosa* (giant star coral) uses tentacle movement to sweep sediments away from the tissues. *Siderastrea radians* can persist for long periods of time buried in sediment (Lirman et al. 2002). In recent experiments (Vargas-Angel 2005), *Siderastrea siderea, Montastraea cavernosa*, and *Solenastrea bournoni* (n=4 specimens for each species) were exposed to sediment accumulations of 1.5 mm per day for four weeks. Observations included visual and histopathological evaluations resulting in a stress index, with scores of 1 for normal, normal (no stress) to 5 for advanced morbidity. Most of the corals were severely compromised after 14 days, displaying an inability to remove sediment, loss of tissue color, and lack of tentacle extension (polyp retraction), as well as tissue atrophy and loss, accumulations of intracellular debris, and reduced tissue integrity. By four weeks, the stress index for the three species ranged from 1.5 to 4.

Acropora spp. appear to be particularly sensitive to sediment rain and shading effects from increased sediment regimes. Because these corals are almost entirely dependent upon sunlight for nourishment compared to massive, boulder-shaped species (Porter 1976, Lewis 1977), they are much more susceptible to increases in water turbidity and sedimentation than other species. Dredging or other pollution that reduces long-term water clarity can reduce the ratio of production to respiration below unity. If this occurs, *Acropora* spp. may not be able to compensate with an alternate food source such as zooplankton (Porter 1987). Both *A. cervicornis* and *A. palmata* are generally unable to remove coarser sediments (250-2000 μm) and only weakly able to remove finer sediments (62-250 μm) (Hubbard and Pocock 1972). However, water movement (turbulence) and gravity are probably more important in removing sediments from these species than their capabilities of sloughing sediments in stagnant water (Porter 1987).

Rogers (1983) investigated the effects of sedimentation on *A. cervicornis, A. palmata, Diploria strigosa, D. clivosa*, and *Montastraea annularis*. *Acropora palmata* was the least tolerant of sediment exposure, 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 *A. cervicornis* facilitated passive sediment removal, making this species more tolerant of sediment accumulation. In another experiment, Rogers (1979) shaded a 20 m^2 area of reef and found that *A.*

cervicornis (the most abundant species in this area; 45% of the total living corals) was the first to respond to shading. Three weeks after shading was initiated, most colonies of *A. cervicornis* were devoid of color (bleached). Shading was terminated after 5 weeks. After six weeks, the growth tips of the *A. cervicornis* 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.

Thus, high sediment loads can have lethal and sub-lethal effects on both *A. palmata* and *A. cervicornis*. It is likely that regulatory controls on land-use prevent sedimentation from posing a more serious threat in many areas.

African Dust

Shinn et al. (2000) proposed that atmospheric dust transported largely from Africa has severely affected Caribbean coral-reef organisms. This hypothesis is based largely on the occurrence of *Aspergillus sydowii* in dust samples, a fungus known to be a pathogen affecting two sea fans (*Gorgonia ventalina* and *G. flabellum*) (Geiser et al. 1998). To date, the two identified (*Serratia marcescens*) or suspected (*Vibrio charcharia*) pathogens of acroporids have not been identified among the microbes in dust (Griffin et al. 2003).

Carbon Dioxide

The potential effects of increased atmospheric CO_2 were summarized in section 4.6.2.3. Currently there are no in situ studies that confirm the laboratory results that have shown declines in calcification associated with ocean acidification. Recent modeling by McNeil et al. (2004), which does not incorporate loss due to bleaching at temperature extremes, suggests that gradual warming of ocean water along the Great Barrier Reef will be more beneficial to calcification than the detrimental effects of ocean acidification. While this model incorporates both GCC and atmospheric CO_2 increase, it does not account for temperature extremes (as discussed in section 4.6.2.1 and section 6) and therefore predicts that by 2100 coral calcification will exceed pre-industrial rates by about 35%.

Nutrients

Nutrients are delivered to coral reefs from both point source (readily identifiable inputs where pollutants are discharged to receiving surface waters from 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 discharge, and groundwater. These source routes may also bring other stressors (e.g., sediments, turbidity, contaminants) that are discussed in other sections of this document. As human activities in coastal regions have increased, nutrient discharge has increased as well. However, natural oceanographic sources like internal waves and upwelling also distribute nutrients on coral reefs, and these natural sources may account for more material (nitrogen and phosphorus) than anthropogenic sources in highly developed areas such as the Florida Keys (Leichter et al. 2003). Notably, the reefs in the Florida Keys are exceptional in that they are located relatively far from land compared to most other reefs in the Caribbean.

Coral reefs have been generally considered to be nutrient-limited systems, meaning that levels of accessible nitrogen and phosphorus limit the rates of plant growth. When nutrients levels are raised in such a system, plant growth can be expected to increase and this can yield imbalance and changes in community structure. Because corals contain small symbiotic algae within their tissues (zooxanthellae), nutrient enrichment can disrupt the symbiosis (Dubinsky and Stambler 1996), thereby affecting metabolic processes, coral growth, and reproductive success. For example, field experiments have shown decreased fecundity and fertilization success in Pacific *Acropora* spp. subjected to slight increases in nitrogen concentrations in the water column (or phosphorus for fertilization) (Ward and Harrison 2000, Harrison and Ward 2001). Increased growth rates of free-living reef algae (e.g., turfs and seaweeds) might be expected to yield higher abundances and overgrowth of reef substrates. Indeed, the widespread increase in seaweed abundance on coral reefs has been attributed to nutrient enrichment (e.g., Bell 1991, Lapointe 1997). However, seaweed abundance on coral reefs is also regulated by herbivores and recent experimental evidence suggests that seaweed proliferation is more directly linked with reduced herbivory (e.g., Diaz-Pulido and McCook 2003, McClanahan et al. 2003). The role of nutrient enrichment in reef community shifts remains controversial (Hughes et al. 1999, Lapointe 1999, McClanahan et al. 2004, Szmant 2002).

Sea Level Rise

While it is assumed that coral reef growth should be able to keep pace with projected rates of future sea-level rise, this upward growth may be affected by elevated temperature, degraded water quality as a result of sea-level rise, and ocean acidification as a result of increased CO_2. Although few studies have examined these effects specifically on Atlantic *Acropora* spp., it is generally assumed that processes associated with GCC will affect most stony corals including the three being reviewed here. However, the projected effects of GCC have not been observed to date, and the majority of the population decline observed during the 1980s and 1990s was principally due to disease, hurricanes, vessel groundings, and predation.

Clionid Sponge Boring

A very different sort of space competition is imposed on *A. palmata* and *A. cervicornis* by the bioeroding sponges of the genus *Cliona* (Photos 28a-b). These sponges exercise what could be classified as interference competition for space, as they actively invade and kill live corals, including *Acropora* spp., to make the space their own. In some geographic areas, the incidence of *Cliona*-induced mortality can be substantial. The degree of invasion by *Cliona* has been linked to human sewage pollution (Rose and Risk 1985); and therefore, has been suggested as a good indicator for sewage impacts on coral reef systems. Sponges are filter-feeders, so organic enrichment of reef waters may enhance clionid growth and productivity. However, clionid infestations are also common in some areas remote from human populations (e.g., Navassa).

Invasion of acroporid skeletons by *Cliona* has a chronic or persistent effect on ecosystem function beyond the point of mortality, as sponge boring greatly increases the susceptibility to breakage and erosion of complex reef frameworks. Thus, *Acropora*-

constructed reef habitat will be less persistent in situations where *Cliona* is common, either as an active agent of coral mortality or as a subsequent invader of dead skeletons.

Contaminants

This section will focus on toxic and bioactive contaminants, while nutrients and other sewage-related stresses are discussed 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 organisms' tissues (reviewed in Peters et al. 1997). However, the analytical ability to detect contaminant substances in low concentrations sheds little insight on the effect these substances might have on the corals themselves (i.e., the response). Kendall et al. (1983) exposed *A. cervicornis* 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 *A. cervicornis* 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 perceives and responds to a given stressor. 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 *A. cervicornis* 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 (Negri and Heyward 2001) and settlement (Reichelt-Brushett and Harrison 2000) of different Pacific *Acropora* spp. Most recently, 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). 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. Thus, it is impossible at current levels of knowledge to prioritize the level of threat that contaminants pose.

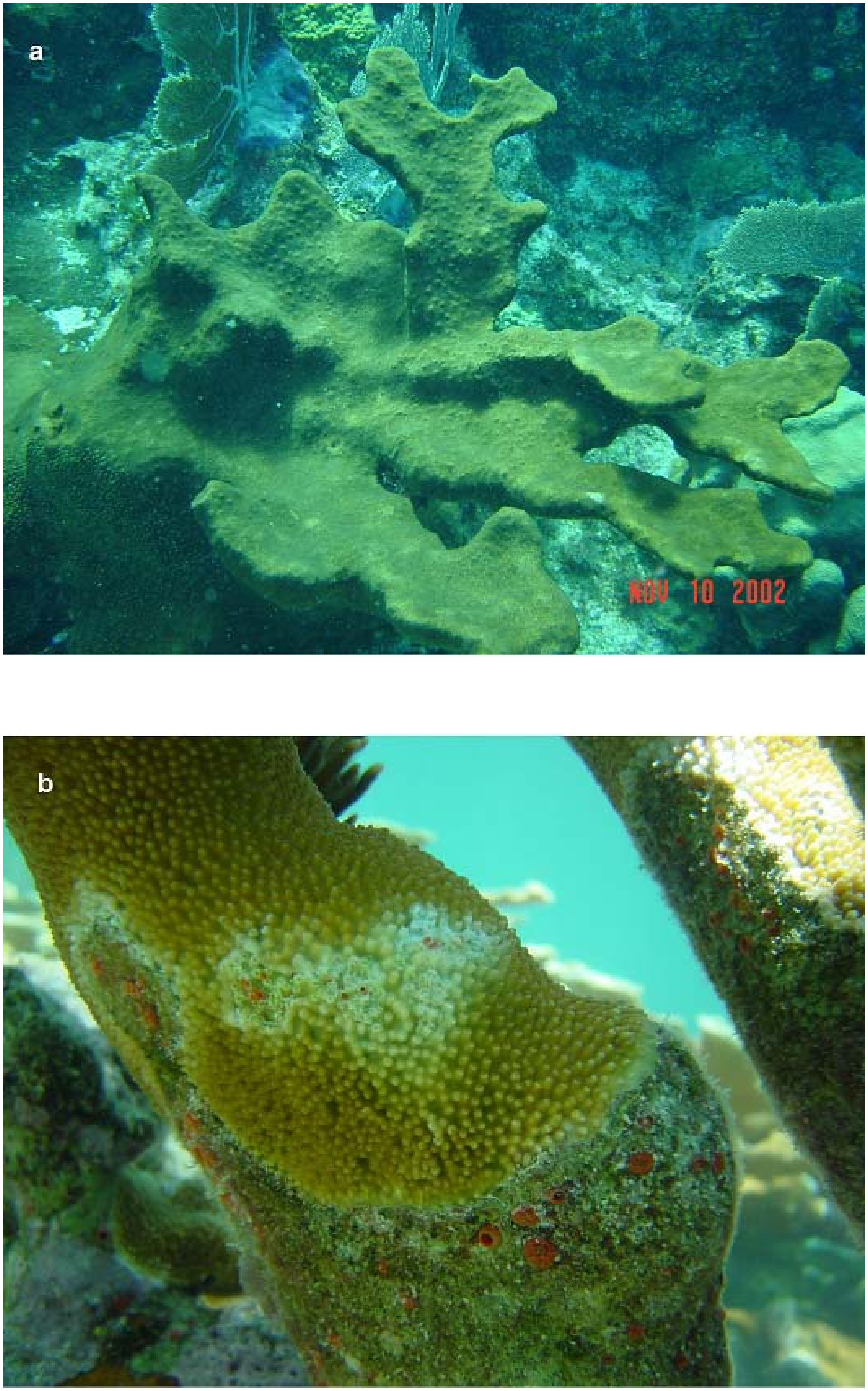


Photo 28. Examples of two species of *Cliona*, boring sponge, preying upon *Acropora palmata*. In (a) the colony has been completely consumed by *Cliona sp*. Photo credits M. Miller.

Loss of Genetic Diversity

Genetic diversity is important in providing scope for populations to adapt to environmental changes. Reduced genetic diversity often results when species undergo rapid decline like *A. palmata* and *A. cervicornis* have in recent decades. This expectation is heightened when the decline is due to a potentially selective factor such as disease, in contrast to a less selective factor such as hurricane damage, which will likely cause disturbance independent of genotype. A species may preserve 90% or more of its original genetic diversity after a severe bottleneck if subsequent recovery is exponential. If the species remains at low densities for prolonged periods of time, genetic diversity may be significantly reduced. Thus, given the dominance of asexual reproduction, the rapid decline (largely from a selective factor), and the lack of rapid recovery that have characterized *A. palmata* and *A. cervicornis*, 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. No quantitative information is available regarding genetic diversity for either species.

The only quantitative information available on genotypic diversity is from recent sampling of *A. palmata*. *Acropora palmata* has been shown to retain moderate to high levels of genotypic diversity in many geographic areas. In some areas, specifically, the Florida Keys, there are very low levels of genotypic diversity (Baums et al. in press a and unpubl. data). Because the levels of diversity prior to the rapid population declines are unknown, it is impossible to know if this represents a localized loss. There is no quantitative information available on genotypic diversity for *A. cervicornis* but many places throughout the range retain multiple genotypes (Vollmer and Palumbi in prep).

6.2 Inadequacy of Existing Regulatory Mechanisms

In order to assess the final listing factor of the ESA (factor D = the inadequacy of existing regulatory mechanisms), the BRT ranked the potential impact of each stressor to *A. palmata* and *A. cervicornis* on a regional (Caribbean Sea) scale without and with protections and prohibitions afforded by federal and state regulations (Table 8). All rankings were based on the current state of each species (abundance and distribution) and level of stress with the realization that some of these threats (e.g., sea level rise and CO_2) will likely continue, and even increase in the future. It is important to note that certain stressors (e.g., nutrients or predation) were ranked relatively low in Table 8 due to consideration of the threat level throughout the species' geographic range (i.e., entire wider Caribbean). However, these same stressors may pose high levels of threat to local populations (e.g., point-source pollution in Barbados or vessel groundings in U.S.V.I.) and therefore should not be discounted.

It is apparent from Table 8 that current regulations are indeed providing some measure of management of the threats to these species, since many times the impact of a stressor was less (as indicated by a reduction in rank in varying degrees) when efficacy of regulations was considered. Notably, some of the greatest threats (i.e., those with the highest ranking such as disease, temperature and natural abrasion and breakage from hurricanes) are not likely manageable, at least at current levels of knowledge, as they are in part naturally occurring phenomena whose impacts are likely elevated due to the cumulative effects of threats to the species as discussed further in section 6.3.

Table 8. Rank of stressor severity to *Acropora palmata* and *A. cervicornis* on a regional scale without (w/out) and with (w/) prohibition/protection of existing regulatory mechanisms (regs). A rank of 5 represents the highest threat, 1 the lowest, and U undetermined/unstudied. Sources of each stressor are listed in Table 5.

Stressor	*A. palmata*		*A. cervicornis*	
	Rank w/o Regs	Rank w/ Regs	Rank w/o Regs	Rank w/ Regs
Disease	5+	5+	5+	5+
Temperature	5	5	5	5
Over-harvest	5*	1	5*	1
Natural abrasion and breakage	4	4	4	4
Anthropogenic abrasion and breakage	3	2	2	1
Competition	3	3	3	3
Predation	3	3	3	3
Sedimentation	3	2	3	2
African Dust	1	1	1	1
CO_2	1	1	1	1
Nutrients	1	1	1	1
Sea level rise	1	1	1	1
Sponge boring	1	1	1	1
Contaminants	U	U	U	U
Loss of genetic diversity	U	U	U	U

*Threat of over-harvest to *A. palmata* and *A. cervicornis* was projected and evaluated on absence of regulation (i.e., level of threat due to over-harvest if collection was not prohibited).

6.3 Synergistic Effects

Scientific knowledge of many of these individual stressors (e.g., disease, contaminants) is often not as precise or as extensive as we would like. However, it is even less clear what the cumulative effects of these threats might be. Some documentation of pattern and experimental research indicates that the cumulative or interactive effects of multiple individual threats are greater than their sum. For example, it has been demonstrated that predators of *Acropora* spp, the snail *Coralliophila abbreviata*, which can have important impacts on depressed populations by themselves, can also vector disease (Williams and Miller in press). Thus, a population of *A. palmata* that is subject to a high predator load may have enhanced disease impacts as well as direct predation impacts.

Another example is that there are numerous aspects of GCC that are anticipated to interact with other threats. Bleaching is the most direct mode of impact expected from climate warming (Hoegh-Guldberg 1999), in turn, impairing colony growth and reproduction (Goreau and Macfarlane 1990; Omori et al. 2001) even after recovery. Additionally, some climate models suggest that GCC is likely to increase hurricane activity and hence, increased physical damage to acroporid populations. There are also observations from diverse geographical locations of coral disease outbreaks following hurricane disturbances (Puerto Rico, Bruckner and Bruckner 1997; Navassa, Miller, pers. observ.; Bonaire, Bruckner pers. comm.; Curaçao, Vermeij pers. comm.; Honduras , Halley et al. 2001). Specifically, Knowlton et al. (1981) describes mass mortality of *A. cervicornis* following Hurricane Allen in Jamaica, and Bythell et al. (2000) describe increased prevalence of disease-associated mortality following hurricanes in the U.S.V.I. However, there is no evidence regarding mechanism(s) that may explain this linkage of hurricane and disease impacts. It is plausible that abrasive stress from storms makes corals more susceptible to infection, and that resident pools of pathogens (e.g., concentrated in pockets of reef sediment) could be mobilized by storms.

Perhaps the greatest concern for the persistence and recovery of Atlantic *Acropora* spp. within the realm of GCC is the interaction of rising temperature coupled with coral disease virulence and the potential for the emergence of new diseases (Harvell et al. 1999). Outbreaks of coral disease have been reported to coincide with temperature induced bleaching events (Jones, et al. 2004). Recent laboratory experiments show that corals affected by so-called yellow band disease (which does not affect *Acropora* spp.) suffer significantly greater rates of mortality at increased temperature (i.e., 32^{o}C) than either unaffected corals at 32^{o}C or affected corals at moderate temperature (Cervino, et al. 2004). More specific mechanistic understanding of how microbial pathogens are affected by temperature has been provided for another non-*Acropora* spp. disease, the bacteria *Vibrio shiloi* that affects temperate corals in the Mediterranean Sea. This bacterial pathogen can adhere to host cells (in order to infect) and survive in the oxygen-rich environment inside the host cell only at higher temperatures (>28^{o}C), while at lower temperatures it is not pathogenic (summarized in Rosenberg 2004). While no such specific information has been determined for diseases affecting *Acropora* spp., warm temperatures correlate with increased incidence of WPx disease on *A. palmata* (Patterson et al. 2002, Rogers and Muller, Figure 10 in the section 9). Thus, colonies subject to heat stress are likely to be coping with bleaching and disease at the same time.

The possibility that new diseases might emerge in the future under a warming temperature regime is also of great concern. New diseases can emerge when environmental conditions, or geographic or habitat ranges shift (Harvell, et al. 1999). Shifts in environmental conditions (such as increased temperature) can increase the susceptibility of a host or the virulence of a potential pathogen. Global climate change may also yield geographic shifts in habitat range that could bring novel pathogens in contact with *Acropora* spp. Though no information is available on the loss of genetic diversity in Atlantic *Acropora* spp., the fact that they have persisted at drastically reduced abundance over a long time frame favors the possibility that genetic diversity has been lost and this compromises these species' ability to adapt to novel pathogens (Frankham 1995).

Although the interaction of individual stressors is difficult to study in a rigorous, controlled experimental manipulation, it is clear that *Acropora* spp. corals are facing a myriad of threats, some of which might be new, (i.e., outside of the species evolutionary experience such as contaminants or novel pathogens). It is also clear that the corals are experiencing many of these stressors in new and severe combinations and it is logical to conclude that the synergistic effects of these combined stressors represent a larger threat than any individual stressor by itself.

7 Prognosis for Persistence and Recovery

Many factors including both intrinsic life history characteristics as well as external threats are important to consider in assessing extinction risk. Recovery of *A. palmata* and *A. cervicornis* from their current levels of decreased abundance obviously depends upon rates of recruitment and growth outpacing rates of mortality. These species have rapid growth rates and high potential for propagation via fragmentation. However, while fragmentation is an excellent life history strategy for recovery from physical disturbance, it is not as effective when fragment sources (i.e., large extant colonies) are scarce. Thus, it is anticipated that successful sexual reproduction will need to play a major role in Atlantic *Acropora* spp. recovery (Bruckner 2002). Meanwhile, there is substantial evidence to suggest that sexual recruitment of both *A. palmata* and *A. cervicornis* is currently compromised. Reduced colony density in these broadcast-spawning, self-incompatible species, compounded in some geographic areas with low genotypic diversity suggests that fertilization success and consequently, larval availability has been reduced. In addition, appropriate substrate available for fragments to attach to is likely reduced due to changes in benthic community structure on many Caribbean reefs. Coupled with impacts from coastal development (i.e., dominance by macroalgal, turf, and/or sediment-coated substrates), these factors are expected to further reduce successful larval recruitment below an appropriate scale that can compensate for observed rates of ongoing mortality.

Recruitment of new colonies on localized reefs is being reported in areas throughout the Caribbean (e.g., Florida Keys, U.S.V.I., Mexico, Venezuela, and Colombia). However, a common pattern has also been observed that these small colonies suffer high rates of complete or partial colony mortality. For example, Sutherland and Ritchie (2004) reported the recruitment and subsequent loss of new fragments, while Williams and Miller (2005) reported high rates of recent juvenile (whole colony) mortality for both *A. palmata* (11% over 18 months, n=65) and *A. cervicornis* (10% over 18 months, n=68) in the Florida Keys. Therefore, in some areas with vigilant monitoring, recruitment of *Acropora* spp. is occurring, but is not necessarily leading to recovery.

Species at reduced abundance are at a greater risk of extinction due to stochastic environmental and demographic factors (e.g., episodic recruitment factors). *Acropora palmata* and *A. cervicornis* have persisted at extremely reduced abundance levels (in most areas with quantitative data available, less than 2% of prior abundance) for at least two decades. This pattern suggests that the prognosis for persistence is reasonably good, but the prognosis for recovery is quite poor. *Acropora palmata* and *A. cervicornis* clearly remain at risk from demographic and environmental stochasticity due to persistently low abundance throughout most if not all of their range. In some areas such as the Florida Keys, abundance of these species has continued to decline into the late 1990s and early 2000s, well beyond the primary loss in the early 1980s.

Meanwhile, the threats to *A. palmata* and *A. cervicornis* persistence and recovery are severe, ongoing, synergistic, and have displayed an increasing trend in the recent past. Disease, which is determined to be the greatest threat to *Acropora* spp. persistence and recovery, is widespread, episodic and unpredictable in its occurrence, and results in high amounts of mortality. Both the total number of described coral diseases (Harvell et al. 1999), as well as the prevalence and/or geographic range of white pox affecting *A. palmata* (Weil 2004), have increased over the past decade and it is logical to assume that this trend will continue. The number of hurricanes impacting Caribbean reefs has increased over the past two decades. Gardner et al. (2005), in a meta-analysis of hurricane impacts using 67 separate Caribbean reef monitoring studies, found 2 hurricanes in the 1970s, 6 hurricanes in the 1980s, and 12 hurricanes in the 1990s affected reefs under study during that period. Sea surface temperature is expected to continue rising over time and this implies increasing threat to *A. palmata* and *A. cervicornis* persistence from bleaching-induced mortality (Hoegh-Guldberg 1999) and, possibly, exacerbation of disease impacts. Increases in human population densities and activity levels in coastal areas are bound to persist, implying increases in the moderate threats posed by direct human interaction (e.g., groundings, diver interactions, coastal construction or dredging, etc.). Since there is no reason to expect this trend of increasing frequency and/or intensity of stressors to abate, we expect the level of threat to these two species to increase over the next decade.

Lastly, because the important threats to persistence and recovery of Atlantic *Acropora* spp. are poorly understood (i.e., disease) and/or difficult or impossible to manage, they should be deemed as representing a higher level of risk to species survival than if, for example, human harvest was a primary threat, in which case greater confidence could be placed in the effectiveness of future management measures (e.g., harvest regulation). In the meantime, managing some of the stressors ranked as less severe by the BRT (e.g., nutrients, sedimentation) may assist in decreasing the rate of *A. palmata* and *A. cervicornis* decline by enhancing coral condition and decreasing synergistic stress effects. This situation also dictates that research efforts should be intensified to determine causal and mechanistic aspects of disease, contaminant impacts, and their interaction with rising temperatures in order to elucidate potential management or mitigative measures.

Given these considerations of moderate intrinsic potential for recovery but severe and worsening extrinsic threats, the BRT agreed that the likelihood for recovery, and perhaps persistence, for both *A. palmata* and *A. cervicornis* is likely to decline in the near future. For these reasons, the BRT concludes that *A. palmata* and *A. cervicornis* are not currently at risk of extinction but are likely to become so, within the foreseeable future.

8 Evaluation of Non-regulatory Measures

Restoration

Acropora spp. are well known for their ability to generate new colonies from fragments (Tunnicliffe 1981, Highsmith 1982, Kobayashi 1984, Wallace 1985, Harriott and Fisk 1988, Fong and Lirman 1995). Studies (Tunnicliffe 1981, Bowden-Kerby 2001a,b) document that *A. cervicornis, A. palmata*, and *A. prolifera* fragments will grow and generate a new colony under suitable circumstances (water quality must be sufficient to support the organisms, low predator pressure, location of the fragment is not in unfavorable habitat, e.g., silty sediments). *Acropora cervicornis* and *A. prolifera* fragments with axial corallites grow rapidly and have less mortality relative to fragments that lack axial corallites (Bowden-Kerby 2001a, b). Extension rates in all *Acropora* species are greater than virtually all other Scleractinian species.

Therefore, there is potential for using *Acropora* spp. fragments in active restoration. In some cases, this takes the form of "rescuing" fragments which are created by some physical disturbance, particularly ship groundings, by re-attaching them to appropriate substrates in the damaged area. In other cases, fragments are used to enhance or re-populate areas where *Acropora* spp. (usually *A. cervicornis*) were known to have previously formed extensive thickets. Prior to the early 1980s when *Acropora* spp. were at high abundance, human investment in *Acropora* restoration was unheard of. The fact that we consider, and often invest extensive resources in husbanding *Acropora* spp. fragments, is one indicator of the radical decline that has taken place in the past few decades.

A documented effort to re-attach *A. palmata* fragments occurred following the Fortuna Reefer ship grounding at Mona Island, Puerto Rico in 1997. Almost 2000 *A. palmata* fragments were re-attached in the grounding site with wire. This is not a standard attachment technique, but was implemented because the high swells at the affected site precluded the use of more typical cement. Two years later, 57% of the restored fragments retained live tissue, 26% were completely dead, and 17% were lost (Bruckner and Bruckner 2001). Along with fragment loss, typical natural sources of mortality such as disease, predation, infestation by boring sponges, etc. affected the restored fragments. Also, few of the fragments (14%) had actually fused to the substrate, suggesting that most of the survivors were still susceptible to future loss in the case of additional wire failure (Bruckner and Bruckner 2001).

In the past two years, three large vessels have struck reefs in Virgin Islands National Park that have had an impact on *A. palmata*. Two of the vessels struck Johnson's Reef off the north shore of St. John. Both impacted a number of *A. palmata* colonies, which necessitated the reattachment of many fragments to nearby dead *A. palmata* colonies. These fragments are being monitored for reattachment, growth and mortality. The Pesca Nostra site is adjacent to Watermelon Cay off Leinster Bay. This vessel destroyed one large *A. palmata* colony. Due to the absence of any nearby dead *A. palmata* colonies, fragments were left in situ and are being monitored for "natural" reattachment and success.

A new approach for re-establishing grounding-generated *A. palmata* fragments, dubbed Reef Crowns, has been implemented at a site in the Florida Keys National Marine Sanctuary. This technique involves an 117-cm circular pre-cast concrete ring capped with 20- to 30-cm irregular limestone rocks embedded 8 to10 cm in the upper layer of the ring. This ring is placed on a flat reef substrate, two long rebar stakes are driven into the reef in the center of the ring, and a cement/sand grout is used to backfill the center of the ring, bonding to the reef substrate. Fragments of *A. palmata* are quickly "planted" into the grout. Twenty such reef crowns were deployed at Western Sambo reef in 2002 (Photo 29). All were unaffected by Hurricane Frances in 2004 and all the *A. palmata* fragments are healthy and growing.

Photo 29. Reef Crown restoration module, two years post deployment, Connected Site, Western Sambo, FKNMS. Photo credit H. Hudson.

Proactive restoration projects in Puerto Rico are seeking to implement the approach developed by Bowden-Kirby (2001a,b). Donor *A. cervicornis* fragments are gathered from healthy populations and then attached to wire mesh frames in protected environments. The fragments overgrow the wire structures fairly rapidly to form miniature “thickets”. These restored *A. cervicornis* units in protected environments can serve as nurseries to provide fragments for creating additional mini-thickets in areas where *A. cervicornis* was known to have flourished in recent times, and to enhance fish habitat.

In early 2002, the approval of a port in Punta Caicedo, Boca Chica, Dominican Republic included the destruction of over 300 colonies of adult *A. palmata* that lie in the channel. However, local community protest, combined with a developer's desire to avoid controversy, resulted in the adoption of large-scale transplantation measures to protect the *A. palmata*. Scientists from the University of Costa Rica and the Dominican National Aquarium and Ministry of Environment were contracted to train local divers in coral transplantation methods and to initiate the project in which 300 colonies were transplanted in November 2002. The colonies (previously physically undisturbed *A. palmata* all with 100% live coral tissue cover) were transplanted from their location at an international port construction site to a hurricane-damaged reef located approximately 1500 m upstream of the port. Depending on size, the colonies were re-attached using Portland type II cement, stainless steel wire, and/or tiewraps. Preliminary results after approximately 1 year yield a survival rate of 95%, and an average growth rate of 3.0 to 3.5 cm/yr. Live coral coverage estimates are approximately 70 to 80% (Bezy pers. comm.). All of the colonies have overgrown their wire connectors and 95% have fused with the substrate.

Mooring Buoy Programs

Mooring buoys have been shown to be an effective management tool when used to minimize damage to coral reefs and other sensitive marine resources resulting from careless or inappropriate anchoring practices. The goals of the FKNMS Mooring Buoy Program are to:

1. Minimize impacts to sensitive marine habitats, specifically coral reef formations, caused by the inappropriate use of anchors;
2. provide reasonable access to sanctuary resources, consistent with the primary goal of resource protection; and
3. manage or restrict human activities where such activities are found to have a detrimental impact on sanctuary resources.

In the FKNMS, mooring buoys are designed for short-time use and employ an embedment-type anchor that holds the buoy securely in place without damaging nearby corals. In 1981, the first experimental embedment anchor mooring system in the Florida Keys was installed (Halas 1985). Later, different embedment anchors were developed for different substrates, such as the "Manta Ray" anchor for sand bottom (Halas 1997). Using start-up expertise from the sanctuary program, several non-profit organizations have installed additional mooring buoys. There are nearly 400 mooring buoys in the FKNMS.

International information and training transfer has been ongoing since September 1986 when the Cayman Islands began establishing a buoy system based on the Florida Keys embedment anchor system. This system is now being used worldwide in more than 50 countries or regions and usage continues to increase in both number of installations and number of regions using the system.

The Virgin Islands National Park established its mooring program in an effort to provide safe anchorage to visiting boaters while protecting important seagrass and coral reef communities. Qualitative observations suggest that there has been an increase in and regeneration of seagrass around many of the moorings in the park. Currently there are 215 moorings within the Virgin Islands National Park and 19 within the Virgin Islands Coral Reef National Monument.

On St. Thomas the Reef Ecology Foundation has installed approximately 60 moorings at coral reef dive locations around the island and offshore cays. These moorings have a three-hour time limit and are not for overnight use. On St. Croix an organization named DIVERSe VIRGIN, Inc. is made up of an alliance of all dive operators on the island. These dive operators use approximately 50 moorings that have been installed around the island at major dive sites. The nonprofit organization Island Conservation Effort through Project Anchors Away oversees the installation and maintenance of these moorings with volunteer help from the dive shops. Also on St. Croix, the newly established East End Marine Park plans to install approximately 100 moorings to protect benthic habitats.

Navigation Measures

Several designations that limit vessel operations and various navigational aids help protect coral reefs from vessel groundings and other impacts. The 1990 designation of the FKNMS included a prohibition on the operation of tankers and other vessels longer than 50 m (164 ft) in four "Areas To Be Avoided (ATBAs)" within and near the boundary of the sanctuary. In 2001, eight Racon radar transponder beacons were installed in the FKNMS to help ships avoid grounding on coral reefs. The devices emit unique signals that appear on ship radar, enabling mariners to precisely identify the location of navigational aids, and warn ships that they are nearing a reef.

The sea around the Florida Keys is one of seven Particularly Sensitive Sea Areas (PSSA) that has been designated by the International Maritime Organization. A major benefit of this designation, which became official in December 2002, is that it provides international recognition of the ATBAs and no-anchoring zones on the Tortugas Bank.

The FKNMS Waterway Management Program includes a comprehensive and effective waterway marking and management system for boaters within the sanctuary. In addition to markers, this program incorporates several surveys and databases that aid in waterway management. The databases include several studies of propeller scar data, the location of existing markers (permitted and unpermitted), the location and function of marine facilities, depth of entrance and exit channels from subdivisions throughout the Keys, and a vessel grounding database.

The Virgin Islands National Park (VINP) maintains a number of navigational aids to prevent vessels from striking underwater objects, including coral reefs. These aids range from boat exclusion buoys around shallow reefs, seagrass areas and beaches, to larger, lighted discretionary buoys around offshore reefs. Buoys have prevented, in many cases, vessels from striking reefs and producing significant damage.

Outreach/Education

In the FKNMS, education and outreach have played a primary role in resource protection. The FKNMS Education and Outreach Program seeks to raise conservation awareness among target audiences, positively affect public attitudes, and increase the value people place on the Florida Keys ecosystem. Some examples of education and outreach activities include:

- Coral Reef Classrooms, reaching 3,314 students in nine years
- Organizing and conducting Adult Environmental Education events
- Distributing educational materials to businesses
- Helping to found and leading the statewide Seagrass Outreach Partnership to raise awareness of the significance of seagrass beds
- Publishing the *Florida Keys Dive and Snorkel User's Guide*

The U.S.V.I. Department of Planning and Natural Resources, Division of Fish and Wildlife, has an environmental education program designed to produce educational materials for use by island teachers. Materials include videos, posters, brochures, coloring books, etc. that are designed to educate islanders and visitors on the value and issues related to the natural environment in the U.S.V.I. Many of the materials include coral reef protection and preservation information.

Numerous other agencies and private organizations (Sea Grant, The Ocean Conservancy, Division of Coastal Zone Management, etc.) also produce and disseminate educational/outreach materials that relate to coral reef protection.

U.S. Coral Reef Task Force

The United States Coral Reef Task Force (USCRTF) was established in 1998 by Presidential Executive Order #13089 to lead U.S. efforts to preserve and protect coral reef ecosystems. The USCRTF includes leaders of twelve federal agencies, seven U.S. states and territories, and three freely associated states. The USCRTF has been instrumental in building partnerships and strategies for on-the-ground action to conserve coral reefs. NOAA as a partner in the USCRTF submitted *A National Coral Reef Action Strategy* (http://coris.noaa.gov/activities/actionstrategy/action_reef_final.pdf) to Congress to help track implementation of *The National Action Plan to Conserve Coral Reefs* developed by the USCRTF in 2000. The National Action Plan: (1) identified key threats and issues driving the loss and degradation of coral reefs, (2) established thirteen major goals to address these threats, and (3) outlined objectives and priority actions needed to achieve each goal. *Acropora* spp. was not specifically mentioned in the document, however many of the issues discussed apply to the acroporids. Additionally, the USCRTF identified the need for Local Action Strategies (LAS), which are locally-driven roadmaps for collaborative and cooperative action among federal, state, territory and non-governmental partners which identify and implement priority actions needed to reduce key threats to valuable coral reef resources. The draft LASs for Southeast Florida, Puerto Rico and U.S.V.I. are available (www.coralreef.gov).

Non-governmental Organizations

Numerous non-governmental organizations (NGO) support coral research, monitoring, restoration and protection. Those that specifically protect *Acropora* spp. have been discussed in other sections of this report. For a relatively exhaustive list of coral-centric NGOs visit the International Coral Reef Information Network (ICRIN) website (www.coralreef.org).

- ReefKeeper International has its Caribbean Region office in Puerto Rico. They are very active in monitoring federal and local actions as they pertain to protection of corals and coral reefs in the US Caribbean. They always provide comments on management actions proposed by the Caribbean Fishery Management Council and others that may have an effect on corals.
- Coralations is based in Puerto Rico and is active in community-based efforts to educate local populations on the value of coral reefs, impacts to coral reefs and efforts to protect them.
- Island Resources Foundation (IRF) in the U.S.V.I. and British Virgin Islands has been involved in many efforts to protect and preserve coral reef areas throughout the Caribbean through research and education. IRF operates on grant monies and donations from the private sector.

International Coral Reef Initiative (ICRI)

The International Coral Reef Initiative (ICRI) is a partnership among governments, international organizations, and non-government organizations created in 1994. Is goal is to protect coral reefs and related ecosystems by implementing Chapter 17 of Agenda 21, and other relevant international conventions and agreements

National Coral Reef Institute (NCRI)

The primary goal of the National Coral Reef Institute (NCRI) is the protection and preservation of coral reefs through applied and basic research on coral reef assessment, monitoring, restoration, and biodiversity, as well as via training and education. This goal is addressed through multidisciplinary scientific research on coral reef assessment, mitigation, monitoring, and restoration as directed by Congress, as well as through applied engineering, operations, and public education.

Summary of Evaluation of Non-regulatory measures

Although there are many outstanding efforts being implemented to conserve and restore corals, and *Acropora* spp. specifically, these activities are likely only addressing minor anthropogenic threats (i.e., anchor damage, vessel strikes). No efforts can be envisioned at this time to abate the impacts of the major threats (i.e., those with the highest ranking such as disease, temperature and natural abrasion and breakage from hurricanes). In all likelihood, the current conservation efforts being enacted via the plethora of non-regulatory activities listed above are unable to keep pace with the drastic decline these species are experiencing.

9 Research

While identifying information needs at the 2002 Caribbean *Acropora* workshop (Bruckner 2002), numerous gaps were realized relative to recovery efforts and effective management of human activities. Key research areas identified during the 2002 workshop were as follows:

- The basic biology of these corals, with an emphasis on reproduction and recruitment;
- The geologic time scales and linkages among past mortality events and recent declines with respect to human and other disturbances;
- The etiology of coral diseases;
- Genetic studies including linkages among populations, genetic exchange between populations, and effects of disturbances on genetic diversity;
- Scientific information on demographic parameters and habitat-based variables;
- Evaluation of strategies to enhance recovery, including propagation and translocation into degraded areas and techniques to mitigate threats.

One of the key information needs that is currently lacking is a model for colonial (modular) organisms that incorporates life history traits, demographic parameters, and threats and is capable of providing a reliable method to predict the current risk of extinction Atlantic *Acropora* spp. face and the potential for this to continue into the future.

The topical areas discussed in the information needs section (9.2) focus on the urgency to identify and quantify critical habitat, current and historical extents of the species, identify changes that have occurred over different temporal scales (i.e., recent vs. geologic), and to determine the stability of extant populations and the factors that influence stability/persistence. Current and ongoing research in summarized in section 9.1.

9.1 Current

Diadema Restoration

Ken Nedimyer and Martin Moe (Florida Keys National Marine Sanctuary Advisory Council members) conducted a pilot project on *Diadema* restoration in the upper Florida Keys starting in the fall of 2001. Juvenile *Diadema* were translocated from areas with relatively high settlement and extensive winter mortality (reef crest rubble zones) to nearby patch reefs (two experimental and two controls) at densities approaching those on Florida reefs before the *Diadema* die-off of 1983. The average densities of urchins over the 15-month study were 1.7/m^2 and 1.1/m^2 on the two experimental reefs.

NOAA's NURC conducted a rapid habitat assessment of the four reefs before translocation of the urchins and one year afterward. Changes in community composition of the experimental and control reefs reflected some of the changes that have occurred where populations of *Diadema* have increased in abundance naturally (Edmunds and Carpenter 2001). These included increased stony coral and coralline algal cover and decreased macroalgal cover on the experimental reefs (http://floridakeys.noaa.gov/research_monitoring/reports/diadema/diadema.html).

Genetics

Molecular genetic tools are now available to determine the genotype of individual *A. palmata* and *A. cervicornis* colonies. This capacity makes tractable the elucidation of a large range of other types of questions that are important to the evaluation of risk and recovery potential. These questions range from definitive determination of patterns of sexual vs. asexual recruitment to determining the possible existence of disease-resistant genotypes in natural populations. It may also provide guidance on transplanting efforts so that natural genetic and genotypic diversity may be preserved.

Restoration

There is certainly room for great advance in human capacity to enhance or restore coral reefs in general or *Acropora* spp. populations in particular. First, we need to do a much better job of evaluating the success of existing coral reef restoration projects, including those in which fragments of *Acropora* spp. have been re-attached or otherwise manipulated (e.g., Fortuna Reefer site, Western Sambo reef crowns) as well as projects where groundings have removed *A. palmata* and only structural restoration was completed (e.g., Columbus Iselin and Wellwood sites in FKNMS). Does *A. palmata* recruit to concrete/limestone restoration structures in these sites, and does it do so to a greater or lesser degree than to natural undisturbed reef substrates or to "unrestored" substrates? Such evaluation efforts need to incorporate both unimpacted and impacted but unrestored controls, and will allow an objective determination of cost/benefit. In 2004, Hudson and his colleagues initiated a monitoring program at the *Wellwood, Columbus Iselin, Connected, Jaqulyn L, Elpsis*, and *Alec Owen Maitland* restoration sites. They should be able to capture recruitment and success of the transplanted *A. palmata.*

The other potential route for increasing *Acropora* spp. populations is by use of sexually produced planktonic larvae rather than fragments. The advantage of this approach is that source material is potentially orders of magnitude more abundant as each colony (which could yield only a few fragments even if they were actively harvested) may produce thousands of larvae and thus provide for much larger scales of reseeding. Also, sexually produced recruits provide for genetic mixing within the population in contrast to fragmentation where only one or a few genotypes are propagated. The main disadvantage is that it is very difficult to do, as spawning occurs on only one or few nights per year, the larvae are sensitive and difficult to culture, and survivorship of the settlers is quite low. Research is underway to develop methods to address these difficulties in *A. palmata*, but progress is slow (Miller and Szmant in review). In 2004 researchers in the Florida Keys successfully raised a large culture of viable *A. palmata* larvae, which were settled onto reef rubble (Photo 30). Approximately 400 *A. palmata* settlers on approximately 50 rubble pieces were epoxied onto reef restoration structures at the Wellwood site in the FKNMS (Photo 31). Their survivorship will be evaluated at a later time when they are expected to have grown to a size that would be visible in the field (>1 yr).

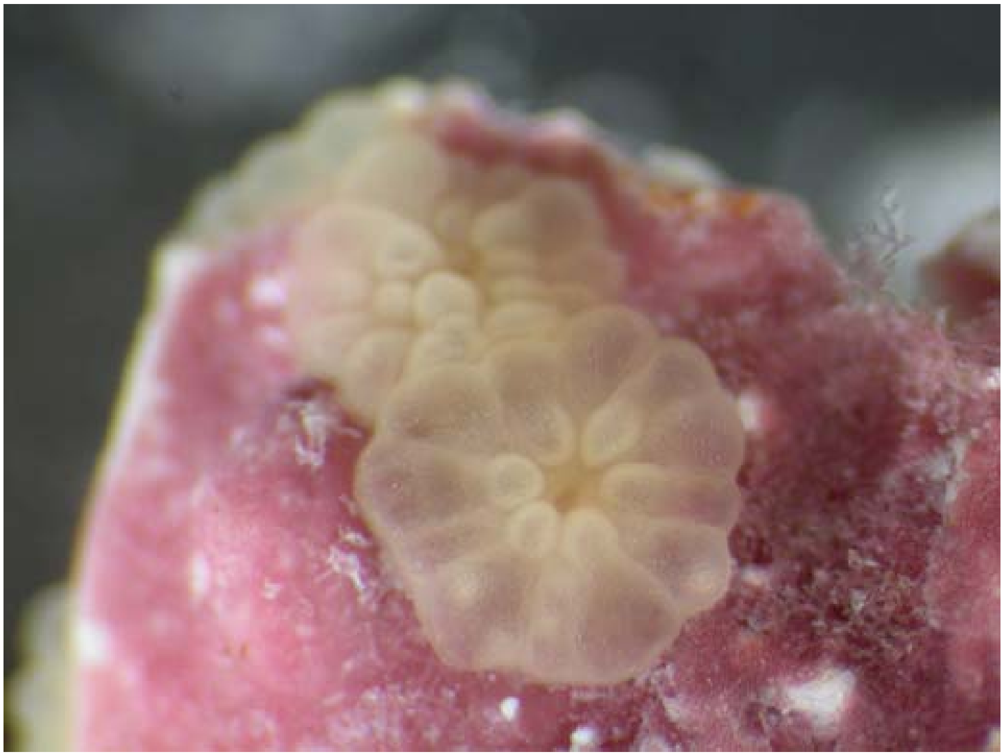


Photo 30. An *Acropora palmata* just settled/metamorphosed on reef rubble in the lab. Photo credit A. Szmant.

Photo 31. Reef rubble with lab-settled *Acropora palmata* attached to restoration structure at Wellwood grounding site, Florida Keys. Photo credit M. Miller.

Another area of research that merits further development is the role of chemical cues in crustose coralline algae (CCA) that may enhance larval settlement on particular substrates. Recent work by Steneck has suggested that individual species of CCA may be crucial for successful larval recruitment in the field. There may be potential to apply either specific chemical derivatives to reef substrates or an "ecological engineering" approach to shift to CCA species composition of reef benthos toward the attractive species in order to stimulate recruitment of *Acropora* spp. larvae in degraded reef areas.

Disease

The single biggest cause of *A. palmata* and *A. cervicornis* mortality has been and continues to be disease. Therefore, all aspects of disease in *Acropora* spp. require monitoring and research attention in order to (1) understand the patterns, prevalence, and impact of disease, (2) determine environmental correlates of disease to suggest how environmental changes may be exacerbating disease impacts, and (3) determine the causes (both proximal and ultimate) of the major diseases affecting *Acropora* spp. in order to begin to plot mitigative and control measures. These goals sound straightforward, but their accomplishment is greatly hampered by the difficulties with disease nomenclature and field diagnosis. For example, some predation scars are difficult to differentiate from diseases, and WBD Type II, recently reported from *A. cervicornis*, can be impossible to distinguish from WBD Type I in the field. In addition, some coral colonies exhibit rapid loss (over several days) of extensive amounts of tissue leaving dead areas that do not resemble the gross signs described for either of the two well-described diseases (WBD or WPx, Photo 20b). A major and necessary effort being coordinated by the Coral Disease and Health Consortium (CDHC) is to standardize the terminology and field signs that are employed in coral disease research (Woodley et al. 2003).

In addition to this CDHC effort, much empirical work is underway. Specifically, targeted monitoring programs are quantifying abundances of colonies with and without disease using randomly and haphazardly selected transects, creating maps of distribution (diseased and unaffected colonies) using GPS technology, and following the fate of individual coral colonies (and individual lesions) with photographs and in situ observations. Overall, it appears that WPx is causing more mortality of *A. palmata* coral than WBD. WBD, as it is currently recognized, is having much greater impact (i.e. mortality) on *A. cervicornis* than *A. palmata*. There is strong evidence that lesions from WPx can heal, or can expand and merge with other lesions until the entire colony is dead. In a few cases, colonies of *A. palmata* have died back over 95%, and then the remnant tissues have begun to grow back over the dead colony.

For example, scientists with USGS, the National Park Service, and the University of the Virgin Islands are mapping stands of living *A. palmata* in three national parks (Virgin Islands National Park, Biscayne National Park, Buck Island Reef National Monument) using GPS technology, and doing research on the stresses that could prevent or delay recovery of this species. Limited recovery has occurred, and *A. palmata* is now more abundant in all three of these national parks than it was 10 years ago. However, the populations are still far below levels seen in the 1970s to early 1980s, and many factors have the potential to reverse this limited recovery, particularly WPx disease and physical damage from boats and hurricanes (most recently Hurricane Ivan). Monthly monitoring of *A. palmata* colonies is occurring at two locations in St. John; in Haulover Bay about 75% of the corals surveyed since February 2003 have had disease, and in Hawksnest Bay about 40% have had disease since May 2004 (Figure 10). At Haulover, 15% of the colonies have died from disease. Additional information on distribution and prevalence of disease .has been collected from 12 other reefs around the island. Prevalence of white pox ranged from less than 1% to 33.8%. USGS and NOAA scientists are examining samples from diseased *A. palmata* to look for presence of bacteria or viruses and histopathological changes in coral tissues.

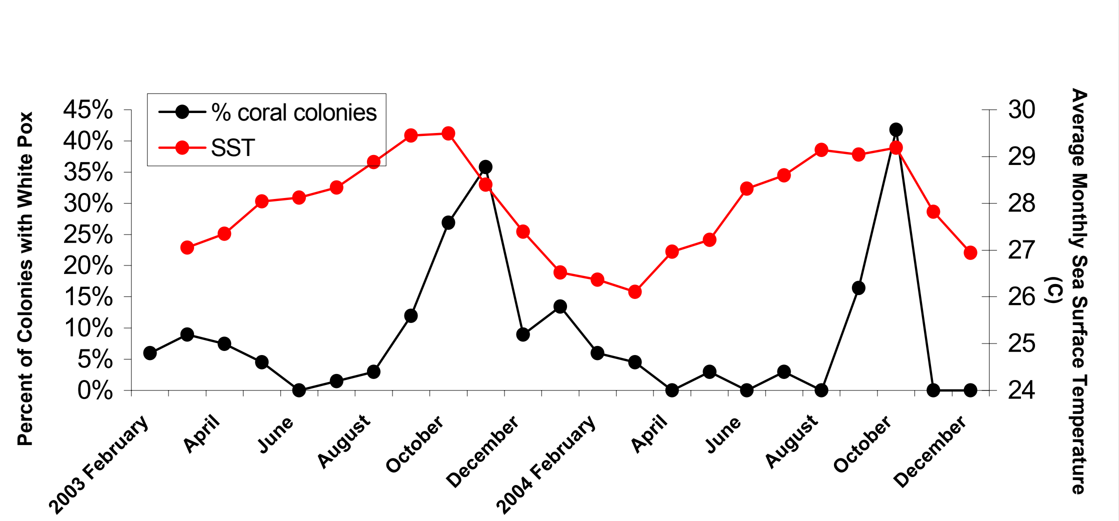


Figure 10. Prevalence of *Acropora palmata* colonies with active white pox lesions at Haulover Bay, St. John, U.S.V.I. in relation to mean monthly sea surface temperature (SST). Data from Rogers and Muller (unpublished).

Much wider-scale sampling of patchy necrosis lesions to confirm or deny their association with *S. marcescens* will help clarify cases which look similar but are not associated with this pathogen. Coordinated microbial and field efforts are also underway to determine if a specific *Vibrio* bacterium (*V. carchariae*) can fulfill Koch's postulates as the causal agent of WBD Type II. Other groups are working to identify the pathogens or groups of pathogens associated with patchy necrosis and WBD. Some *A. palmata* colonies are exhibiting lesions that do not grossly resemble either of these major diseases. Concentrated effort is needed to determine the relationship of stressful environmental conditions and disease outbreaks.

Field transmission experiments are being undertaken to verify the identity of diseases affecting *Acropora* spp. For example, is WBD really the same condition in *A. palmata* and *A. cervicornis*? Or, put another way, what does patchy necrosis/WPx (which is described only for *A. palmata*) look like if it is transmitted to *A. cervicornis* (Williams and Miller in prep.). Field experiments can also investigate other modes of disease transmission, such as predators. Recent work has demonstrated that a virulent outbreak of disease in *A. cervicornis* in the Florida Keys was transmissible by *Coralliophila abbreviata*, the corallivorous snail, indicating that predation and disease may interact in a way that poses even greater threat to persistence and recovery.

Molecular Biomarkers

One current areas of research that has promise for pinpointing or diagnosing specific causes of stress includes the area of molecular biomarkers. Concentrations of a range of cellular products with known functions (e.g., protein degradation) can be feasibly measured. It is believed that the individual profiles for this range of parameters can be used to diagnose precise sources of organismal stress (e.g., a particular environmental toxin). Preliminary work in this area has focused on examining these profiles for healthy colonies over normal seasonal cycles, as well as stressed (e.g., bleached) colonies (Downs et al. 2000, Downs et al. 2002). One study examined specific levels of gene expression in response to pesticide exposure in *A. cervicornis* (Morgan and Snell 2002). One of these gene products appears to have some specificity for organophosphate exposure. Specific ground-truthing with laboratory dose/response experiments remains to be done to validate the diagnostic potential of this approach.

9.2 Needs

Much of the information presented on research needs for Atlantic *Acropora* spp. is summarized from Bruckner (2002). Recommendations stemming from this workshop focused on information needs for supporting recovery efforts and effective management of Atlantic *Acropora* spp. and addressed four topical areas:

- Remote sensing, aerial photography, and geographic information systems (GIS)
- Historical/geological questions and studies
- Research and monitoring needs
- Strategies to enhance recovery

These topical areas highlight the need to quantify critical habitats for these corals; current and historical distribution and abundance patterns; changes that have occurred over different time scales; and the factors influencing the trajectory of extant populations.

Remote sensing (e.g., satellite, aerial photography, acoustic mapping, LIDAR)

There is a need to compile existing maps, historical and current aerial photographs, bathymetric information, airborne sensor data, and other types of information showing existing and potential habitats for Atlantic *Acropora* spp. Such information should be incorporated into a GIS to delineate critical habitats and to aid in the design of appropriate conservation strategies to protect these areas. The topics below highlight the information that is needed on critical habitat, historical distribution, and the current extent of Atlantic *Acropora* spp. The working group report on information needs in Bruckner (2002) summarizes the logistical issues associated with these information needs.

- Identify and map habitats currently occupied by Atlantic *Acropora* spp., as well as those that supported these corals in the recent past. Such maps would ideally include information on bathymetry, physical oceanography, water quality, and substrate type.
- Identify the habitats in terrestrial and marine environments whose protection would maintain/conserve important ecological linkages with key areas of current Atlantic *Acropora* spp. growth.

Notably, remote sensing can not provide data for all aspects of coral research and should be used as a tool to enhance laboratory and field research.

Historical/geological questions and studies

There is a need to improve the understanding of the nature of recent Caribbean-wide declines in Atlantic *Acropora* spp. populations, and whether evidence for causes of historical (geological) declines are evident in fossil *Acropora*. Such information would be useful for assessing whether recent trends are part of a natural cyclical process or whether human stressors are the root cause.

- Larger, regional scale coring programs are needed to compile a long-term record of temporal changes in Atlantic *Acropora* spp. distribution to compare to recent changes.
- To place these longer-term geologic records into context, there is a need to improve our understanding of the nature of recent declines in these corals from agents including, but not limited to, diseases, predation, temperature stress, and water quality degradation.

Research and monitoring needs

To assist in the potential recovery of Atlantic *Acropora* spp., more scientific information is needed on both demographic and habitat-based variables, specifically:

- Survival and fecundity by age and frequency distribution by size structure;
- The relative importance of sexual versus asexual reproduction in populations;
- Which populations are genetically distinct, what are minimum viable population sizes for these corals, and what are the amounts and rates of genetic exchange among populations?
- What are the survivorship and growth rates of juvenile stages of these species and how do habitat variables affect recruitment and adult survivorship?

Additional information needs are:

- Individual colonies at different life stages should be monitored in comparative studies across a range of environmental conditions and human impacts. This information establishes a context for assessment, mitigation, and restoration activities that may be undertaken to conserve/restore Atlantic *Acropora* spp. populations.

- Greater efforts are needed to monitor and assess populations at local to regional scales, including tracking individual colonies through different life stages under different environmental conditions.

Settlement/Recruitment/Reproduction

As summarized in Bruckner (2002), the current scientific capability to assess the potential for recovery of existing Atlantic *Acropora* populations by sexual reproduction and recruitment is impaired by the lack of knowledge in different aspects of the life histories of these species. Specifically, key research areas include:

- Spatial and temporal patterns of gamete formation, fertilization, and release;
- Colony-size thresholds for gamete production;
- Within and among colony variability in gamete production;
- Fertilization patterns;
- Transport and duration of larval stages;
- Larval survivorship patterns;
- Larval settlement requirements and preferences of coral planulae;
- Early survivorship and growth of sexually produced recruits.

Diseases

Very little is known regarding the root causes of coral diseases, given the lack of understanding of basic etiology. As discussed earlier, the pathogenic cause of WBD has not been determined; in addition, the number or identity of specific disease conditions affecting Atlantic *Acropora* spp. and the causal factors involved are uncertain. Diseases of Atlantic *Acropora* spp. will likely prevent or delay recovery of these species, thus there is a clear need to identify the specific mechanisms and gain predictive understanding of diseases.

Strategies to enhance recovery

This topical area focuses on whether restoration of Atlantic *Acropora* spp. is feasible, and the practical issues of propagation/transplantation as a means of enhancing recovery and maintaining existing populations. First and foremost, the goals of mitigation or restoration should be established prior to any action. Second, eliminating or reducing the known human stressors should be a prerequisite to restoration, including the causes and consequences of diseases. Participants at the 2002 Caribbean *Acropora* workshop concluded that:

> *Reef restoration at any scale will have, at best, very limited success unless the causes of decline are understood and action is taken to reduce these threats* (Bruckner 2002).

However, the participants also concluded that:

> *Transplantation and propagation of Atlantic Acropora spp. colonies is a viable tool to enhance recovery at local (reef-site) scales, but considerations such as appropriate selection of colonies and fragments, the potential effects on genetic*

> *structure of populations, and the potential benefits must be weighed against the probability of natural recovery, other management interventions, and likelihood of long-term success* (Bruckner 2002).

Therefore, to facilitate attempts at recovery:

- Information is needed on the genetic structure of Atlantic *Acropora* spp.
- More demographic modeling data are needed to predict the response of populations to future disturbances and stressors at various spatial and temporal scales.

10 Conclusion

This completes the BRT's state of the Atlantic *Acropora* spp. This comprehensive status review, as compiled and deliberated by the BRT, incorporates and summarizes the best available scientific and commercial data to date.

List of References

Adams RD (1968) The leeward reefs of St. Vincent, West Indies. J Geol 76: 587-595

Adey WH (1977) Shallow water Holocene bioherms of the Caribbean Sea and West Indies. Proc 3rd Intl Coral Reef Symp 2: xxi-xxiii

Adey WH (1978) Coral reef morphogenesis: A multidimensional model. Science 202: 831-837

Adey WH, Adey PJ, Burke R, Kaufman L (1977) The Holocene reef systems of Eastern Martinique, French West Indies. Atoll Res Bull 218: 1-40

Adey WH, Burke RB (1977) Holocene bioherms of Lesser Antilles – Geologic control of development. AAPG Studies in Geology 4: 67-81

Agassiz A (1882) Explorations of the surface fauna of the Gulf Stream under the auspices of the United States Coast Survey II. The Tortugas and Florida Reefs. Mem Acad Arts Sci Centennial 2: 107-134

Alcala AC, Gomez ED (1987) A direct test of the effects of protective management on abudance and yield of tropical marine resources. J Cons Int Explor Mer 46: 40-47

Almy CCJ, Carrion-Torres C (1963) Shallow-water stony corals of Puerto Rico. Carib J Sci 3: 133-162

Anderson M, Lund H, Gladfelter EH, Davies M (1986) Ecological community type maps and biological community descriptions for Buck Island Reef National Monument and proposed marine park sites in the British Virgin Islands. U.S. National Park Service and Virgin Islands Resource Management Cooperative. Bioisphere Reserve Report No. 4 236 p

Antonius 1980

Antonius A, Weiner A, Halas J, Davidson E (1978) Looe Key Reef Resource Inventory. Florida Reef Foundation, Homestead, FL

Appeldoorn RS, Recksiek CW, Hill RL, Pagán FE, Dennis GD (1996) Marine protected areas and reef fish movements: The role of habitat in controlling ontogenetic migrations. Proc 8th Intl Coral Reef Symp 8:1917-1922

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

Aronson RB, Precht WF (2001a) Evolutional paleoecology of Caribbean coral reefs. In: Allmon,WD, Bottjer DJ (eds) Evolutionary paleoecology: The ecological context of macroevolutionary change. Columbia University Press, NY pp171-233

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

Auster PJ, Langton RW (1999) The effects of fishing on fish habitat In: Benaka LR (ed) Fish habitat: essential fish and rehabilitation. AFS Symp 22, Bethesda MD pp 150-178

Baggett LS, Bright TJ (1985) Coral recruitment at the East Flower Garden Reef. Proc 5th Intl Coral Reef Congr 4: 379-384

Bak RPM (1975) Ecological aspects of distribution of reef corals in the Netherlands Antilles. Bijdr Dierk 45: 181-190

Bak RPM (1977) Coral reefs and their zonation in the Netherland Antilles. AAPG Stud Geol 4: 3-16

Bak RPM, Criens SR (1982) Survival after fragmentation of colonies of Madracis mirabilis, *Acropora* palmata and *A. cervicornis* (Scleractinia) and the subsequent impact of a coral disease. Proc 4th Intl Coral Reef Symp 1: 221-227

Bak RPM, Elgershuizen JHBW (1976) Patterns of oil-sediment rejection in corals. Mar Biol 37: 105-113

Bak RPM, Engel M (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar Biol 54: 341-352

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

Baker AC, Starger CJ, McClanahan TR, Glynn PW (2004) Coral reefs: Corals adaptive response to climate change. Nature 430: 741

Barker E, Elderfield H (2002) Foraminiferal calcification response to glacial-interglacial changes in atmospheric CO_2. Science 297: 833-835

Baums IB, Hughes CR, Hellberg M (in press a) Mendelian microsatellite loci for the Caribbean hard coral *Acropora palmata*. Mar Ecol Prog Ser

Baums IB, Miller MW, Hellberg ME (in press b) Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. Mol Ecol

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

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

Becker LC, Mueller E (2001) The culture, transplantation, and storage of *Montastraea faveolata, Acropora cervicornis*, and *Acropora palmata*: what have we learned so far. Bull Mar Sci 69: 881-896

Bell PRF (1991) Status of eutrophication in the Great Barrier Reef lagoon. Mar Pollut Bull 23: 89-93

Benaka LR (1999) Fish Habitat: essential fish habitat and rehabilitation. AFS Symp 22, Bethesda MD

Bengtsson L, Botzet M, Esch M (1996) Will greenhouse gas-induced warming over the next 50 years lead to higher frequency and greater intensity of hurricanes? Tellus, 48A:57-73

Bessat F, Buigues AD (2001) Two centuries of variation in coral growth in massive Porities colony from Moorea (French Polynesia): A response of ocean-atmosphere variability from south central Pacific. Paleogeog Paleoclimat Paleoecol 175: 381-392

Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc 3rd Intl Coral Reef Symp 1: 15-21

Blainville HM (de 1830) Zoophytes in Dictionnaire des Sciences naturelles. Paris 60: 295-364

Blanchon P, Shaw J (1995) Reef drowning during the last deglaciation: evidence for catastrophic sea-level and ice-sheet collapse. Geology 23: 4-8

Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. Science 277: 509-515

Bohnsack JA, Harper DE, McClellan DB, Sutherland PL, White MW (1987) Resource survey of fishers within Looe Key National Marine Sanctuary. NOAA Tech Memo NOS MEMD 5.

Bouchon C, Bouchon-Navarro Y, Louis M, Laborel J (1985) Influence of the degradation of coral assemblages on the fish communities of Martinique (French West Indies). Proc Gulf Carib Fish Inst 38: 452-468

Bourne GC (1900) Anthozoa in Treatise of Zoology II. Lankester (ed) London.

Bowden-Kerby A (2001a) Coral transplantation modeled after natural fragmentation processes: low-tech tools for coral reef restoration and management. PhD Dissertation Univ Puerto Rico, Mayaguez

Bowden-Kerby A (2001b) Low-tech reef restoration methods modeled after natural fragmentation processes. Bull Mar Sci 69: 915-931

Brawley SH, Adey WH (1977) Territorial behavior of the three spot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. Environ Biol Fishes 2: 45-51

Bright TJ, Kraemer GP, Minnery GA, Viada ST (1984) Hermatypes of the Flower Garden Banks, northwestern Gulf of Mexico: A comparison to other western Atlantic reefs. Bull Mar Sci 34: 461-476

Broecker WS, Thurber DL, Goddard J, Ku TL, Matthews RK, Mesolella KJ (1968) Milankovitch hypothesis supported by precise dating of coral reefs and seep-sea sediments. Science 159: 297-300

Brook G (1893) The genus *Madrepora*. Brti Mus Nat His Cat Madreporian corals Vol. I, London

Brown BE (1997) Disturbances to reefs in recent times. In: Birkeland C (ed) Life and death of coral reefs. Chapman and Hall, NY pp 354-379

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

Bruckner AW (2002) Proceedings of the Caribbean *Acropora* workshop: Potential application of the U.S. Endangered Species Act as a conservation strategy. NOAA Tech Memo NMFS-OPR-24, Silver Spring, MD

Bruckner AW, Bruckner RJ (2001) Condition of restored *Acropora palmata* fragments off Mona Island, 2 years after the Fortuna Reefer grounding. Coral Reefs 20: 235-243

Bruckner RJ, Bruckner AW, Williams EHJ (1997) Life history strategies of *Coralliophila abbreviata* Lamarck (Gastropoda: Coralliophilidae) on the southeast coast of Puerto Rico. Proc 8th Intl Coral Reef Symp 1: 627-632

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

Budd AF, Johnson KG (1999) Origination preceding extinction during the late Cenozoic turnover of Caribbean reefs, Paloebiology 25: 88-200.

Budd AF, Johnson KG, Stemann TA, Tompkins BH (1999) Pliocene to Pleistocene reef coral assemblages in the Limon group of Costa Rica. In: Collins LS, Coates AG (eds) The Neogene of the Isthmus of Panama: A Paleobiotic survey of the Caribbean coast. Bull Amer Paleont Special Vol 357: 119-158

Buddemeier RW, Fautin DG (1993) Coral bleaching as an adaptive mechanism - A testable hypothesis. Bioscience 43: 320-326

Buddemeier RW, Kleypas JA, Aronson RB (2004) Coral reefs and global climate change: Pew Center on Global Climate Change: 44

Burns TP (1985) Hard-coral distribution and cold-water disturbances in south Florida: Variation with depth and location. Coral Reefs 4: 117-124

Bythell JC, Bythell M, Gladfelter EH (1991) 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. J Exp Mar Biol Ecol 172: 171-183

Bythell JC, Gladfelter EH, Gladfelter WB, French KE, Hillis Z (1989) Buck Island Reef National Monument – changes in modern reef community structure since 1976. In: Hubbard DK (ed) Terrestrial and Marine Geology of St. Croix, U.S. Virgin Islands. West Indies Lab. Spec. Pub. 8, Fairleigh Dickinson University, St. Croix. p 145– 153

Bythell JC, Hillis-Starr ZM, Philips B, Burnett WJ, Larcombe J, Bythell M (2000) Buck Island Reef National Monument, St Croix, US Virgin Islands: Assessment of the impacts of Hurricane Lenny (1999) and status of the reef 2000. National Park Service Report

Cairns SD (1982) Stony corals (Cnidaria: Hydrozoa, Scleractinia) of Carrie Bow Cay, Belize. In: Rutzler K, Macintyre IG (eds) The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. Structure and communities. Smithson Contrib Mar Sci 12: 271-302

Cairns SD, Calder DR, Brinkmann-Voss A, Castro CB, Fautin DG, Pugh PR, Mills CE, Jaap WC, Arai MN, Haddock SHD, Castro DM (2002) Common and scientific names of aquatic invertebrates from the United States and Canada: Cnidaria and Ctenophora. 2nd Ed. AFS Pub 28.

Campbell DG (1977) Bahamian chlorine bleach fishing: a survey. Proc 3rd Intl Coral Reef Symp. 2: 593-596

Caribbean Fishery Management Council (CFMC) (1998) Essential fish habitat (EFH) generic amendment to the fishery management plans (FMRs) of the U.S. Caribbean, including a draft environmental assessment, Vols. I & II. Caribbean Fishery Management Council, San Juan, Puerto Rico

Cervino JM, Hayes RL, Polson SW, Polson SC, Goreau TJ, Martinez RJ, Smith GW (2004) Relationship of Vibrio Species Infection and Elevated Temperatures toYellow Blotch/Band Disease in Caribbean Corals. Appl Env Microbiol 70: 6855-6864

Chalker BE (1977) Daily variation in the calcification capacity of *Acropora cervicornis*. Proc 3rd Intl Coral Reef Symp1: 417-423.

Chalker BE, Taylor D (1978) Rhythmic variations in calcification and photosynthesis associated with the coral *Acropora cervicornis*. Proc R Soc Lond B Biol Sci 201: 179-190

Chiappone M, Dienes H, Swanson DW, Miller SL (2005) Impacts of lost fishing gear on coral reef sessile invertebrates in the Florida Keys National Marine Sanctuary. Biol Conserv 121: 221-230

Chiappone M, Sullivan KM (1996) Distribution, abundance and species composition of juvenile scleractinian corals in the Florida reef tract. Bull Mar Sci 58: 555-569

Chiappone M, Sullivan KM (1997) Rapid assessment of reefs in the Florida Keys: Results from a synoptic survey. Proc 8th Intl Coral Reef Symp 2: 1509-1514

Chiappone M, Sullivan-Sealey KM, Bustamante G, Tschirky J (2001) A rapid assessment of coral reef community structure and diversity patterns at Naval Station Guantanamo Bay, Cuba. Bull Mar Sci 69: 373-394

Chiappone M, Sullivan KM, Lott C (1996) Hermatypic scleractinian corals of the southeastern Bahamas: A comparison to western Atlantic reef systems. Carib J Sci 32: 1-13

Church JA, Gregory JM (2001) Changes in sea level. Climate Change 2001, the Scientific Basis: 639-693

Coles SL, Brown BE (2003) Coral bleaching - capacity for acclimatization and adaptation. Adv Mar Biol 46: 183-223

Connell J (1976) Competitive interactions and the species diversity of corals In: Mackie GE (ed) Coelenterate ecology and behavior. Plenum, NY pp 51-58

Connell, J. H. (1978) Diversity in tropical rain forests and coral reefs. Science 199(4335): 1302-1310.

Cortes J, Guzman HM (1985a) Arrecifes coralinos d la costa Atlantica de Costa Rica. Brenesia 23: 275-292

Cortes J, Guzman HM (1985b) Organismos de los arrecifes coralinos de Costa Rica. III. Descripcion y distribucion geografica de corales escleractinios (Cnidaria: Anthozoa: Scleractinia) de la costa Caribe. Brenesia 24: 63-124

Cortes J, Risk MJ (1984) The coral reef of the Cahuita National Park, Costa Rica. Rev Biol Trop 32: 109-121

Cubit J, Williams S (1983) The invertebrates of Galeta Reef (Caribbean Panama): a species list and bibliography. Atoll Res Bull 259: 1-43

Dana JD (1846) Zoophytes. US Exploring Expedition (Wash) Vol 7

Davis GE (1977) Anchor damage to a coral reef on the coast of Florida. Biol Conserv 11: 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. Bull Mar Sci 32: 608-623

De Freese DE (1991) Threats to biological diversity in marine and estuarine ecosystems of Florida. Coast Mgmt 19: 73-101

Diaz JM, Sanchez JA, Zea S, Garzon-Ferreira J (1996) Morphology and marine habitats of two southwestern Caribbean atolls: Albuquerque and Courtown. Atoll Res Bull 435: 1-33

Diaz-Pulido G, McCook L (2003) Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. Ecology 84: 2026-2033

Donohue M, Boland R, Sramek C, Antonelis G (2001) Derelict fishing gear in the Northwestern Hawaiian Islands: Diving surveys and debris removal in 1999 confirm threat to coral reef ecosystems. Mar Poll Bull 12: 1301-1312.

Douglas AE (2003) Coral bleaching - how and why? Mar Poll Bull 46: 385-392

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

Downs C, Mueller E, Phillips S, Fauth J, Woodley C (2000) A Molecular Biomarker System for Assessing the Health of Coral (*Montastraea faveolata*) During Heat Stress. Mar Biotech 2: 533-544

Dubinsky Z, Stambler N (1996) Marine pollution and coral reefs. Global Change Biol 2: 511-526

Duerdan JE (1902) West Indian Madreporian polyps. Natl Acad Sci Mem 8: 403-648

Dunne RP, Brown BE (1979) Some aspects of the ecology of reefs surrounding Anegada, British Virgin Islands. Atoll Res Bull 236: 1-83

Dustan P (1977) Vitality of reef coral populations off Key Largo, Florida: Recruitment and mortality. Envir Geol 2: 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 Res Bull 288: 1-27

Dustan P (1988) Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1975-1982. NOAA Tech Memo 18

Dustan P (1994) Developing methods for assessing coral reef vitality: A tale of two scales. Pages 38-44 in RN Ginsburg compiler. Proceedings of the colloquium on global aspects of coral reefs: Health, hazards, and history. RSMAS-Univ Miami, FL

Dustan P, Halas JC (1987) Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. Coral Reefs 6: 91-106

Edmunds PJ, Carpenter RC (2001) Recovery of Diadema antillarum reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proc Natl Acad Sci 98: 5067-5071

Ehrenburg CG (1834) Beitrage zur physiologischen Kenntniss der Corallenthiere im allgemeined, und besonders des rothen Meers , nebst einem Versucch zu physiologishen systematic derselben. Phys Abh Konigl Akad Wissech Berlin aus der Jahar 1832: 225-380

Ehrlich PR (1975) The population biology of coral reef fishes. Ann Rev Ecol Syst 6: 211-247

Eldredge LG (1987) Poisons for fishin on coral reefs. In: Salvat B (ed) Human impacts on coralreeefs: facts and recommendations. Antenne de Tahiti Museum EPHE, French Polynesia p 67-76

Enos P (1977) Holocene sediment accumulations of the south Florida shelf margin. In: Enos P, Perkins RD (eds) Quaternary sedimentation of south Florida Part I. Geol Soc Am Mem 147: 1-130

Erhardt H, Werding B (1975) Los corales (Antozoa e Hidrozoa) de la Bahia de Santa Marta, Colombia. Bol Mus de Mar 7: 3-50

Fadlallah YH (1983) Sexual reproduction, development and larval biology in scleractinian corals: A review. Coral Reefs 2: 129 150

Fagerstrom JA (1987) The evolution of reef communities. Wiley, NY

Farrell TM, D'Elia CF, Lubbers L, Pastor LJ (1983) Hermatypic coral diversity and reef zonation at Cayos Arcas, Campeche, Gulf of Mexico. Atoll Res Bull 270: 1-7

Fenner DP (1993) Some reefs and corals of Roatan (Honduras), Cayman Brac, and Little Cayman. Atoll Res Bull 388: 1-30

Fenner DP (1988) Some leewawrd reefs and corals of Cozumel, Mexico. Bull Mar Sci 42: 133-144

Ferr-D'Amare AR (1985) Coral reefs of the Mexican Atlantic: a review. Proc 5th Intl Coral Reef Symp 6: 349-354

Fisk DA, Harriot VJ (1990) Spatial and temporal variation in coral recruitment on the Great Barrier Reef: implications for dispersal hypotheses. Mar Biol 107: 485-490

Fitt WK, Spero HJ, Halas J, White MW, Porter JW (1993) Recovery of the coral *Montastrea annularis* in the Florida Keys after the 1987 Caribbean "bleaching event." Coral Reefs 12: 57-64

Fitt WK, Warner ME (1995) Bleaching patterns of four species of Caribbean Reef Corals. Biol Bull 189: 298-397

Fong P, Lirman D (1995) Hurricane cause population expansion of the branching coral *Acropora palmata* (Scleractinia): wound healing and growth patterns of asexual recruits. Mar Ecol Prog Ser 16: 317-335

Frankham R (1995) Conservation genetics. Ann Rev Genet 29: 305-327

Gardner T, Cote IM, Gill JA, Grant A, Watkinson AR (2005) Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. Ecology 86: 174-184

Garrett P, Smith DL Wilson AO, Patriquin D (1971) Physiology, ecology, and sediments of two Bermuda patch reefs. J Geol 79: 647-668

Gattuso JP, Allemand D, Frankignoulle M (1999) Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review of interactions and control by carbonate chemistry. Amer Zool 39: 160-183

Gayle PMH, Woodley JD (1998) Discovery Bay, Jamaica. CARICOMP – Caribbean coral reef, seagrass and mangrove sites. Coastal region and small island papers 3, UNESCO, Paris

Geister J (1983) Holocene West Indian coral reefs:geomorphology, ecology and facies. Facies, 9,173-284

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

Geister J (1977) The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Proc 3rd Intl Coral Reef Symp 1: 23-29

Getty SR, Asmeron Y, Quinn TM, Budd AF (2001) Accelerated Pleistocene coral extinctions in the Caribbean Basin shown by uranium-lead (U-Pb) dating. Geology 29: 639-642

Ghiold J, Smith SH (1990) Bleaching and recovery of deep-water, reef-dwelling invertebrates in the Cayman Islands, BWI. Carib J Sci 26: 52-61

Gilmore MD, Hall BR (1976) Life history, growth habits, and constructional roles of *Acropora cervicornis* in the patch reef environment. J Sed Petr 46: 519-522

Ginsburg RN, Lowenstam HA (1958) The influence of marine bottom communities on the depositional environment of sediments. J Geol 66: 310-318

Ginsburg RN, Shinn EA (1964) Distribution of reef-building community in south Florida and the Bahamas. Amer Assoc Petr Geol Bull 48: 527

Ginsburg RN, Shinn EA (1994) Preferential distribution of reefs in the Florida reef tract: the past is the key to the present, In: Ginsburg RN (comp) Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History, 1993, RSMAS-Univ Miami, FL pp 21-26.

Gladfelter EH (1982) Skeletal development in *Acropora cervicornis*: I. Patterns of calcium carbonate accretion in the axile corallite. Coral Reefs 1: 45-52

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

Gladfelter EH (1983b) Spatial and temporal patterns of mitosis in the cells of the axile polyp of the reef coral *Acropora cervicornis*. Biol Bull 165: 811-815

Gladfelter EH, Monahan RK, Gladfelter WB (1978) Growth rates of five reef-building corals in the northeastern Caribbean. Bull Mar Sci 28: 728-734

Gladfelter W (1982) White-band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. Bull Mar Sci 32: 639-643

Gleason DF, Wellington GM (1993) Ultraviolet radiation and coral bleaching. Nature 365: 836-838

Glynn PW (1973) Aspects of the ecology of coral reefs in the western Atlantic region. In: Jones OA, Endeans R (eds) Biology and geology of coral reefs, volume 2: Biology 1. Academic Press, NY p 271-324

Glynn PW, Szamt AM, Corocoran EF, Cofer-Shabica SV (1989) Condition of coral reef cnidarians from the northern Florida reef tract: Pesticides, heavy metals and histopathological examination. Mar Poll Bull 20: 568-576

Goldberg WM (1973) The ecology of the coral-octocoral community of the southeast Florida coast: geomorphology, species composition and zonation. Bull Mar Sci 23: 465-488

Goldenberg SB, Landsea CW, Mestas-Nunez AM, Gray WM (2001) The recent increase in Atlantic Hurricane activity: Causes and implications. Science 293: 474-479

Goodwin MH, Cole MJC, Stewart WE, Zimmerman BL (1976) Species density and associations in Caribbean reef corals. J Exp Mar Biol Ecol 24: 19-31

Goreau TF (1959) The ecology of Jamaican reef corals: I. Species composition and zonation. Ecology 40: 67-90

Goreau TF, Goreau NI (1973) Coral Reef Project--Papers in Memory of Dr. Thomas F. Goreau. Bull Mar Sci 23: 399-464

Goreau TF, Goreau NI, Goreau TJ (1979) Corals and coral reefs. Sci Amer 24: 124-136

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

Goreau TJ, Hayes RL, McClanahan.T. (2000) Conservation of Coral Reefs After the 1998 Global Bleaching Event. Cons Biol 14: 5-15

Goreau TJ, Macfarlane, AH (1990) Reduced growth rate of *Montastrea annularis* following the 1987-1988 coral-bleaching event. Coral Reefs 8: 211-215

Goreau TF, Wells JW (1967) The shallow-water Scleractinia of Jamaica: revised list of species and their vertical range. Bull Mar Sci 17: 442-453

Grassle FJ (1973) Variety in coral reef communities. In: Jones OA, Endean R (eds) Biology and geology of coral reefs Vol.2. Academic Press, NY pp 247-270

Graus RR, Chamberland JA, Boker AM (1977) Structural modification of corals in relation to waves and currents. Stud. Geol 4: 135-153

Greenstein BJ, Pandolfi JM (1997) Preservation of community structure in modern coral reef life and death assemblages of the Florida Keys: implications for the Quaternary record of coral reefs. Bull Mar Sci 19: 39-59

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

Guzman HM (1998) Diversity of stony, soft and black corals (Anthozoa: Scleractinia, Gorgonacea, Antipathatia; Hydrozoa: Milleporina) at Cayos Cochinos, Bay Islands, Honduras. Rev Biol Trop (Sup 4): 75-80

Guzman HM, Guevara C (1998) Mortalidad masiva de organismos arrecifales zooxantelados durante el blanqueamiento de 1995 en Cayos Cochinos, Honduras. Rev Biol Trop 46 (Supl 4): 165-173

Halas JC (1985) A unique mooring system for reef management in the Key Largo National Marine Sanctuary. Proc 5th Intl Coral Reef Congr 4: 237-242

Halas JC (1997) Advances in environmental mooring technology. Proc 7th Intl Coral Reef Symp 2: 1995-2000

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

Halley RB, Vacher HL, Shinn EA (1997) Geology and hydrogeology of the Florida Keys. Elsevier, New York (217-248)

Harriot VJ (1985) Recruitment patterns of scleractinian corals at Lizard Island, Great Barrier Reef. Proc 5th Intl Coral Reef Congr 4: 367-372

Harriott VJ, Fisk DA (1987) A comparison of settlement plate types for experiments on the recruitment of scleratinian corals. Mar Ecol Prog Ser 37: 201-208

Harriott VJ, Fisk DA (1988) Coral transplantation as a reef management option. Proc. 6th Intl Coral Reef Symp 2: 375-379

Harrison RS, Coniglio M (1985) Origin of the Key Largo Limestone, Florida Keys; Bull Can Petro Geol. 33: 350-358

Harrison PL, Ward S (2001) Elevated levels of nitrogen and phosphorus reduce fertilization success of gametes from scleractinian reef corals. Mar Biol 139:1057-1068

Harvell CD, Kim K, Burkholder JM, Colwell RR, Epstein PR, Grimes DJ, Hofmann EE, Lipp EK, Osterhaus ADME, Overstreet RM, Porter JW, Smith GW, Vasta GR (1999)

Emerging marine diseases - Climate links and anthropogenic factors. Science 285: 1505-1510

Henderson-Sellers, A, Zhang H, Berz G, Emanuel K, Gray W, Landsea C, Holland G, Lighthill J, Shieh S-L, Webster p, McGuffie K (1998) Tropical cyclones and global climate change: A post-IPCC assessment. Bull Amer Metero Soc 79: 19-38

Heyward A, Stoddart J (1985) Genetic structure of two species of *Montipora* on a patch reef: Conflicting results from electrophoresis and histocompatibility. Mar Biol 85: 117-121

Highsmith RC (1982) Reproduction by fragmentation in corals. Mar Ecol Prog Ser 7: 207-226

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

Hill RL (2001) Post-settlement processes and recruitment dynamics in the white grunt, *Haemulon plumieri*, Lacepède (Pisces: Haemulidae). Ph.D. Dissertation, Univ Puerto Rico, Mayagüez, Puerto Rico

Hixon MA, Beets JP (1989) Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. Bull Mar Sci 44: 666-680

Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol Monogr 63: 77-101

Hoegh-Gulberg O (1999) Climate change, coral bleaching and the future of the worlds coral reefs. Mar Freshwater Res 50: 839-866

Hoffmeister JE, Multer HG (1968) Geology and origin of the Florida Keys. Geol Soc Amer Bull 79: 1487-1502.

Hovland M, Vasshus S, Austdal L, Nilden O (2001) Mapping and imaging deep-sea coral reefs off Norway, 1982-2000. Proc 1st Intl Symp Deepsea Corals p197-198

Hubbard DK, Gill IP, Toscano M, A, (2004) The Holocene *Acropora palmata* record and recent coral-reef decline. College of the Bahamas, Grace Research Center, San Salvador, Bahamas (1-11)

Hubbard J, Pocock Y (1972) Sediment rejection by recent scleractinian corals: a key to paleo-environmental reconstruction. Geol Rundsch 61: 598-626

Hughes TP (1985) Life histories and population dynamics of early successional corals. Proc 5th Intl Coral Reef Symp 4: 101-106

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

Hughes TP, Ayre D, Connell JH (1992) The evolutionary ecology of corals. TREE 7: 292-295

Hughes TP, Connell JH (1999) Multiple stressors on coral reefs: A long-term perspective. Limnol Oceanogr 44: 932-940

Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55: 141-166

Hughes T, Szmant AM, Steneck R, Carpenter R, Miller S (1999) Algal blooms on coral reefs: What are the causes? Limnol Oceanogr 44: 1583-1586

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

Jaap WC (1974) Scleractinian growth rate studies. Proc Fl Keys Coral Reef Wrkshp. FL Dept Nat Res Coastal Coordinating Council p 17

Jaap WC (1979) Observation on zooxanthellae expulsion at Middle Sambo Reef, Florida Keys. Bull Mar Sci 29: 414-422

Jaap WC (1984) The ecology of the south Florida coral reefs: a community profile. US Fish and Wildlife Service (139)

Jaap WC (1985) An epidemic zooxanthellae expulsion during 1983 in the lower Florida Keys coral reefs: Hyperthermic etiology. Proc 5th Intl Coral Reef Congr 6: 143-148

Jaap WC, Halas JC, Muller RG (1988) Community dynamics of stony corals (Millerporina and Scleractinia) at Key Largo National Marine Sanctuary, Florida during 1981-1986. Proc 6th Intl Coral Reef Symp 2: 2370243

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: 31

Jaap WC, Sargent FJ (1993) The status of the remnant population of *Acropora palmata* (Lamark, 1816) at Dry Tortugas National Park, with a discussion of possible causes of changes since 1881. In: Ginsburg RN (comp) Proceedings of the Colloquium on global aspects of coral reefs - health, hazards, and history: RSMAS-Univ Miami, FL. p 101-105.

Jaap WC, Wheaton JW (1975) Observations of Florida reef corals treated with fish collecting chemicals. FL Mar Res Publ 10

Jaap WC,Wheaton JW (1995) Annual report for amendment 5, subagreement CA-5000-09027/1, Cooperative agreement CA-5000-8-8014. US National Park Service, US Dept. Interior. Benthic coral reef monitoring at Dry Tortugas National Park: 1 October 1994 to 30 September 1995. St Petersburg, FL

Jaap WC, Wheaton JW, Callahan M, Hackett K, Kupfner S,Lybolt M (2002) Long Term (1989-Present) Monitoring of Selected Coral Reef Sites at Dry Tortugas National Park. June 2002. Fla. Mar. Res. Inst. Tech. Rep. to Dry Tortugas National Park.

Jackson JBC (1992) Pleistocene perspectives of coral reef community structure. Amer Zool 32: 719-731

Jackson JBC (2001) What is natural in the coastal oceans? Proc Natl Acad Sci 98: 5411-5418

Jennings S, Lock JM (1996) Population and ecosystem effects of reef fishing. In: Polunin NVC, Roberts CM (eds) Reef fisheries. Chapman and Hall, NY pp 193-218

Jennings S, Polunin NVC (1996) Impacts of fishing on tropical reef ecosystems. Ambios 5: 44-49

Johns GM, Leeworthy VR, Bell FW, Bonn MA (2001) Socioeconomic study of reefs in southeast Florida. Hazen and Sawyer, Fl. Lauderdale, FL

Jones RJ, Bowyer J, Hoegh-Guldberg O, Blackall LL (2004) Dynamics of a temperature-related coral disease outbreak. Mar Ecol Prog Ser 281: 63-77

Jones, RJ, Kerswell AP (2003) Phytotoxicity of photosystem II (PSII) herbicides to coral. Mar Ecol Prog Ser 261:149-159

Jones GP, Syms C (1998) Disturbance, habitat structure and the ecology of fishes on coral reefs. Aust J Ecol 3: 287-297

Jones RS, Thompson MJ (1978) Comparison of Florida reef fish assemblages using a rapid visual technique. Bull Mar Sci 28: 159-172

Jordan E, Merino M, Moreno O, Martin E (1981) Community structure of coral reefs in the Mexican Caribbean. Proc 4th Intl Coral Reef Congr 2: 303-308

Jordan-Dahlgren E (1992) Recolonization patterns of *Acropora* palmata in a marginal environment. Bull Mar Sci 51: 104-117

Jordan-Dahlgren E, Rodriguez-Martinez RE (1998) Post-hurricane initial recovery of *Acropora palmata* in two reefs of the Yucatan Peninsula, Mexico. Bull Mar Sci 63: 213-228

Kaufman L (1977) The three spot damselfish: effects on benthic biota of Caribbean coral reefs. Proc 3rd Intl Coral Reef Symp, 1: 559-564

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. Bull Mar Sci 33: 336-352

Kendall MS, Christensen JD, Hillis-Starr Z (2003) Multi-scale data used to analyze the spatial distribution of French grunts, *Haemulon flavolineatum*, relative to hard and soft bottom in a benthic landscape. Environ Biol Fishes 66: 19-26

Kenny JS (1988) Hermatypic scleractinian corals of Trinidad. In: Van der Steen LJ (ed) Studies in honour of Dr. Peter Wagenaar Hummelinck. Foundation for Scientific Research in Surinam and the Netherlands Antilles p 83-100

Kleypas JA, Buddemeier RW, Archer D, Gattuso JP, Langdon C, Opdyke BN (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science 284: 118-120

Knowlton N, Lang JC, Keller BD (1990) Case study of natural population collapse: Post hurricane predation of Jamaican staghorn corals. Smithson Contrib Mar Sci 31: 1-25

Knowlton N, Lang J, Rooney M, Clifford P (1981) Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. Nature 249: 251-252

Knutson TR, Tuleya RE, Shen W, Ginis ! (2001) Impact of CO_2-induced global warming as simulated using the GFDL Hurricane Prediction System. Climate Dynamics 15: 503-519

Kobluk DR, Lysenko MA (1992) Storm features on a southern Caribbean fringing coral reef. Palaios 7: 213-221

Kornicker LS, Boyd DW (1962) Shallow-water geology and environments of Alacran Reef complex, Campeche Bank, Mexico. Bull Amer Assoc Petr Geol 46: 640-673

Koyayashi N (1984) Regeneration and regrowth of fragmented colonies of the hermatypic corals *Acropora formosa* and *Acropora nasuta*. Galaxea 3: 13-23

Kuhlmann DHH (1974) The coral reefs of Cuba. Proc 2nd Intl Coral Reef Symp 2: 69-83

Kuhlmann DHH (1975) Charackterisierung der Korallenriffe von Veracruz Mexiko. Int Rev ges Hydriobiol 60: 495-521

Kushmaro A, Loya Y, Fine M, Rosenberg E (1996) Bacterial infection and coral bleaching. Nature 380: 396

Kushmaro A, Rosenberg E, Fine M, Loya Y (1997) Bleaching of the coral Oculina patagonica by Vibrio AK-1. Mar Ecol Prog Ser 147: 159-165

Lamarck JBP (de 1816) Histoire naturelle des animaux san vertebras. Paris 2: 1-568

Lang JC (1973) Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. Bull Mar Sci 23: 260-279

Lang JC (2003) Status of coral reef in the western Atlantic: Results of initial surveys, Atlantic and Gulf rapid reef assessment (AGRRA) Program. Atoll Res Bull 496

Langdon C (2003) Review of experimental evidence for the effects of CO2 on calcification of reef builders. Proc 9th Intl Coral Reef Symp 2: 1091-1098

Lapointe BE (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnol Oceanogr 42: 1119-1131

Lapointe BE (1999) Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs. Limnol Oceanogr 44: 1586-1592

Lara M, Padilla C, Garcia C, Espejel JJ (1992) Coral reef of Veracruz Mexico I. Zonation and community. Proc 7th Intl Coral Reef Symp 1: 535-544

Leichter J, Stewart J, Miller SL (2003) Episodic nutrient transport to Florida coral reefs. Limnol Oceanogr 48: 1394-1407

Leao ZMAN (1986) Guia para identificacao dos corais do Brasil. Programa de Pesquisa e Pos-Gracuacaoem Geofisica, Instituto de Giociencias, Universidade Federal da Bahia, Salvador. 57 p

Leao ZMAN, Araujo TMF, Nolasco MC (1988) The coral reefs off the coast of eastern Brazil. Proc 6th Intl Coral Reef Symp 3: 339-347

Levitan DR (1991) Influences of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. Biol Bull 181: 261-268

Lewis JB (1974) Settlement and growth factors influencing the contagious distribution of some Atlantic reef corals. Proc 2nd Intl Coral Reef Symp 2: 201-207

Lewis JB (1975) A preliminary description of the coral reefs of the Tobago Cays, Grenadines, West Indies. Atoll Res Bull 178: 1-14

Lewis JB (1977) Suspension feeding in Atlantic reef corals and the importance of suspended particulate matter as a food source. Proc 3rd Intl Coral Reef Symp 1: 405-408

Lewis JB (1981) Coral reef ecosystems. Pages 127-158 in AR Longhurst, ed. Analysis of marine ecosystems. Academic Press, NY

Liddell WD, Ohlhorst SL (1987) Patterns of reef community structure, North Jamaica. Bull. Mar. Sci. 40:311-329

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: 125-130

Lindeman KC (1997) Development of grunts and snappers of southeast Florida: Cross-shelf distributions and effects of beach management alternatives. Ph.D. Dissertation, University of Miami, Miami, FL

Lirman D (1999) Reef fish communities associated with *Acropora palmata*: Relationships to benthic attributes. Bull Mar Sci 65: 235-252

Lirman D (2002) A simulation model of the population dynamics of the branching coral *Acropora* palmata: effects of storm intensity and frequency. Ecol Mod 161: 169-182

Lirman D, Fong P (1997) Patterns of damage to the branching coral *Acropora palmata*: effects of colonization, colony size, lesion size and lesion shape. J Exp Mar Biol Ecol 251: 41-57

Lizama J, Blanquet R (1975) Predation on sea anemones by the amphinomid polychaete *Hermodice carucullata*. Bull Mar Sci 25: 442-443

Logan BW (1969) Carbonate sediments and reefs, Yucatan shelf, Mexico. Am Assoc Petrol Geol Bull Mem 11: 1-199

Logan BW (1969) Coral reefs and banks: Yucatan shelf, Mexico. Mem Amer Associ Petr Geol 11: 129-198

Longhurst AR, Pauly D (1987) Ecology of tropical oceans. Academic Press, NY

Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral *Porities*. J Exp Mar Biol Ecol 245: 255-243

Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. Mar Biol 49: 317-323

Macintyre IG, Glynn PW (1976) Evolution of modern Caribbean fringing reef, Galeta Point, Panama. Amer Assoc Petr Geol Bull 60: 1054-1072

Marquez L, MacKenzie J, Takabayashi M, Smith C, Chen C (2000) Difficulties in obtaining microsatellite markers from acroporid corals. Proc 9th Intl Coral Reef Symp 1: 139-140

Marsden JR (1962) A coral-eating polychaete. Nature 193: 598

Marshall SM, Orr AP (1931) Sedimentation of Low Isles reef and its relation to coral growth. Sci Rep Grt Bar Reef Exp 1: 93-134

Marubini F, Ferrier-Pages C, Cuif JP (2003) Suppression of growth in scleractinian corals by decreasing ambient carbonate ion concentration: A cross-family comparison. Proc Royal Soc Biol Sci 270: 179-184

Mayer AG (1914) The effect of temperature upon tropical marine animals. Carneige Inst Wash Publ 183: 3-24

McClosky L (1970) The dynamics of the community associated with a marine scleractinian coral. Int Rev Gesamten Hydriobiol 55: 13-81

McClanahan T, Sala E, Mumby P, Jones S (2004) Phosphorus and nitrogen enrichment do not enhance brown frondose 'macroalgae'. Mar Poll Bull 48: 196-199

McClanahan T, Sala E, Stickels P, Cokos B, Baker A, Starger C, Jones SI (2003) Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Mar Ecol Prog Ser 261: 135-147

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

McField MD (1999) Coral response during and after mass bleaching in Belize. Bull Mar Sci 64: 155-172

McGehee MA (1994) Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. Mar Ecol Prog Ser 105: 243-255

McNeil BI, Matear RJ, Barnes DJ (2004) Coral reef calcification and climate change: The effect of ocean warming. Geophys Res Lett 31: L22309.

Mesolella KJ, Matthews RK, Broecker RK, Thurber DL (1969) The astronomical theory of climate change: Barbados data. J Geol 77: 250-274

Meyer JL, Schultz ET, Helfman GS (1983) Fish schools: an asset to corals. Science 220: 1047- 1048

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 Tech Memo NMFS-SEFSC-479

Miller MW, Hay ME, Miller SL, Malone D, Sotka EE, Szmant AM (1999) Effects of nutrients versus herbivores on reef algae: A new method for manipulating nutrients on coral reefs. Limnol Oceanogr 44: 1847-1861

Miller MW, Szmant AM (in review) Lessons Learned from Experimental Key-Species Restoration. In: Precht WF (Ed.) Coral Reef Restoration Handbook- The Rehabilitation of an Ecosystem Under Siege. CRC Press.

Milliman JD (1973) Caribbean coral reefs. In: Jones OA, Endean R (eds) Biology and geology of coral reefs, volume 1: Geology 1. Academic Press, NY p 1-50

Moreno et al. 1981 – page 53

Morgan, MB; Snell, TW (2002) Characterizing stress gene expression in reef-building corals exposed to the mosquitocide dibrom. Mar Poll Bull 44: 1206-1218

Morse DE, Hooker N, Morse ANC, Jensen RA (1988) Control of larval metamorphosis and recruitment in sympatric agariciid corals. J Exp Mar Biol Ecol 116: 192-217

Morse ANC, Morse DE (1996) Flypapers for coral and other planktonic larvae. Bioscience 46: 254-262

Morse DE, Morse ANC, Raimondi PT, Hooker N (1994) Morphogen-based chemical flypaper for *Agaricia humillis* coral larvae. Bio Bull (Woods Hole) 186: 172-181

Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, van't Hof T, den Hartog C (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census techniques. Estuar Coast Shelf Sci 51: 31-44

Neigel JE, Avise JC (1983) Clonal diversity and population structure in a reef-building coral, *Acropora* cervicornis: self-recognition analysis and demographic interpretation. Evolution 37: 437-454

Negri AP, Heyward AJ (2001) Inhibition of coral fertilization and larval metamorphosis by tributyltin and copper. Mar Env Res 51: 17-27

Neumann AC, Macintyre IG (1985) Reef response to sea level rise: keep-up, catch-up and give-up. Proc 5th Int Coral Reef Congress 3: 105-110

Newell ND, Imbrie J, Purdy EG, Thurber DL (1959) Organism communities and bottom facies, Great Bahama Bank. Bull Amer Mus Nat Hist 117: 177-228

Nunez Lara E, Arias Gonzalez E (1998) The relationship between reef fish community structure and environmental variables in the southern Mexican Caribbean J Fish Biol 53: 209-221

Ogden JC, Ehrlich PR (1977) The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae). Mar Biol 42: 273-280

Ogden JC, Ogden NB (1998) Reconnaissance survey of the coral reefs and associated ecosystems of Cayos Cochinos, Honduras. Rev Biol Trop 46 (Supl 4): 67-74

Ogden J, Wicklund R (1988) Mass bleaching of coral reefs in the Caribbean: a research strategy. Natl Undersea Res Prog Rep 88-2

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

Omori M, Fukami H, Kobinata H, Hatta M (2001) Significant drop of fertilization of *Acropora* corals in 1999: An after-effect of heavy coral bleaching? Limnol Oceanogr 46: 704-706

Padilla C, 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

Pandolfi JM, Jackson JBC (2001) Community structure of Pleistocene coral reefs of Curaçao, Netherlands Antilles. Ecol Mono 71: 49-67

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*. Proc Natl Acad Sci 99: 8725-8730

Pêcheux M (2002) CO2 increase, a direct cause of coral reef mass bleaching? Mar Life 212: 63-68

Peckol PM, Curran HA, Floyd EY, Robbart ML, Greenstein BJ, Buckman KL (2003) Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Res Bull 496: 146-171.

Peters EC (1984) A survey of cellular reactions to environmental stress and disease in Caribbean scleractinian corals. Helgolander Meeresuntersuchungen 37: 113-137

Peters EC (1997) Chapter 6. Diseases of Coral-Reef Organisms. Chapman and Hall, NY

Peters EC, Yevich PP, Oprandy JJ (1983) Possible causal agent of 'white band disease' in Caribbean acroporid corals. J Invertebr Pathol 41:394–396

Porter JW (1972) Patterns of species diversity in Caribbean reef corals. Ecology 53: 745-748

Porter JW (1976) Autotrophy, heterotrophy, and resource partitioning in Caribbean reef corals. Amer Nat 110: 731-742

Porter JW (1987) Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (south Florida) – Reef-building corals. US Fish Wildl Serv Biol Rep 82(11.73), US Army Corp of Engineers, TR EL-82-4, 23 p

Porter JW, Battey J, Smith G (1982) Perturbation and change in coral reef communities. Proc Nat Acad Sci 79: 1678-1681

Porter JW, Meier OW (1992) Quantification of loss and change in Floridian reef coral populations. Amer Zool 32: 625-640

Porter JW, Woodley JD, Smith GJ, Neigel JE, Battey JF, Dallmeyer DG (1981) Population trends among Jamaican reef corals. Nature 294: 249-250

Precht WF, Miller SL (in press) Ecological shifts along the Florida reef tract: the past as a key to the future. In: Geological approaches to coral reef ecology. Springer Verlag, NY

Prentice IC (2001) The carbon cycle and atmospheric carbon dioxide. Cambridge University Press (183-238)

Ramirez A, de Ramirez IB, Correal JE (1985) Ecologia descriptive de las llaunras madreporarias del Parque Nacional submarine Los Corales del Rosario (Mar Caribe), Colombia. FEN Colombia

Rannefeld JW (1972) The stony corals of Enmedio Reef off Veracruz, Mexico. MS Thesis, Texas A&M University, College Station, TX, 104 p

Reed JK (1985) Deepest distribution of Atlantic hermatypic corals discovered in the Bahamas. Proc 5th Intl Coral Reef Congr 6: 249-254

Richards WJ, Lindeman KC (1987) Recruitment dynamics of reef fishes: Planktonic processes, settlement and demersal ecologies, and fishery analysis. Bull Mar Sci 41: 392-410

Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the tropical Pacific, and the Red Sea. Mar Ecol Prog Ser 60: 185-203

Ridley SO (1884) Report on the zoological collections made in the Indo-Pacific Ocean during the voyage of H.M.S. "Alert", 1881-2. Spongiida. London Brit. Mus. Nal. Hist.,. 366-482, 2: 582-630. 1

Riebesell U, Zondervan I, Rost B, Tortell PD, Zeebe RE, Morel FM (2000) Reduced calcification of marine phytoplankton in response to increased atmospheric CO_2. Nature 407: 364-367

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

Ritchie KB, Smith GW (1998) Type II white-band disease. Rev. Biol. Trop 46 Supl. 5: 199-203

Robbin DM (1981) Subaerial $CaCO_3$ crust: A tool for timing reef initiation and defining sea level changes. Proc 4th Intl Coral Reef Symp 1: 575-579

Roberts HH (1971) Environments and organic communities of North Sound, Grand Cayman Island, BWI. Carib J Sci 11: 67-79

Roberts HH (1972) Coral reefs of St. Lucia, West Indies. Carib J Sci 12: 179-190

Roberts HH, Suhayda JN (1983) Wave-current interactions on a shallow reef (Nicaragua, Central America). Coral Reefs 1: 209-214

Roberts H, Rouse JJ, Walker ND, Hudson JH (1982) Cold-water stress in Florida Bay and northern Bahamas: A product of winter frontal passages. J Sed Petrol 52: 145-155

Roberts HH, Wilson PA, Lugo-Fernandez A (1992) Biology and geologic responses to physical processes: Examples from modern reef systems of the Caribbean-Atlantic region. Cont Shelf Res 12: 809-834

Rodriguez-Martinez RE, Banaszak AT, Jordan-Dahlgren E (2001) Necrotic patches affect *Acropora palmata* (Scleractinia: Acroporidae) in the Mexican Caribbean. Dis Aquat Org 47: 229-234

Rogers CS (1979) The effect of shading on coral reef structure and function. J Exp Mar Biol Ecol 41: 269-288

Rogers CS (1983) Sublethal and lethal effects of sediments applied to common Caribbean reef corals in the field. Mar Poll Bull 14: 378-382

Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. Mar Ecol Prog Ser 62: 185-202

Rogers CS, Fitz HC, Gilnack M, Beets J, Hardin J (1984) Scleractinian coral recruitment patterns at Salt River submarine canyon, St. Croix, U.S. Virgin Islands. Coral Reefs 3: 69-76

Rogers CS, Suchanek T, Pecora F (1982) Effects of Hurricanes David and Frederic (1979) on shallow *Acropora* palmata reef communities: St. Croix, USVI. Bull Mar Sci 32: 532-548

Rogers CS, Sutherland KP, Porter JW (in press) Has white pox disease been affecting *Acropora* palmata for over 30 years? Coral Reefs.

Roos PJ (1964) The distribution of reef corals in Curaçao. Stud Fauna Curaco Carib Isla 20: 1-51

Roos PJ (1971) The shallow-water stony corals of the Netherlands Antilles. Stud Fauna Curaco Carib Isla 37: 1-108

Rose C, Risk M (1985) Increase in *Cliona delitrix* infestation of *Montastrea cavernosa* heads on an organically polluted portion of the Grand Cayman fringing reef. PSZNI: Mar Ecol, 6: 345-362

Rosenberg E (2004) The bacterial disease hypothesis of coral bleaching. In: Rosenberg E, Loya Y (eds) Coral Health and Disease. Springer, Berlin. p 445-459

Rutzler K , Macintyre IG (1982) The habitat distribution and community structure of the barrier reef complex at Carrier Bow Cay, Belize, In: Rutzler K, Macintyre IG (eds) The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize. I. Structure and Communities. Smithsonian Contrib Mar Sci 12, Smithsonian Institution Press, Washington, DC: 9-45

Rylaarsdam KW (1983) Life histories and abundance patterns of colonial corals on Jamaican reefs. Mar Ecol Prog Ser 13: 249-260

Sale PF (1977) Maintenance of high diversity in coral reef fish communities. Amer Nat 111: 337-359

Sale PF (1980) The ecology of fishes on coral reefs. Oceanogr Mar Biol Ann Rev 18: 367-421

Sammarco PW (1980) *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J Exp Mar Biol Ecol 45: 245-272

Sammarco PW (1985) The Great Barrier Reef vs. the Caribbean: Comparisons of grazers, coral recruitment patterns and reef recovery. Proc 5th Intl Coral Reef Congr 4: 391-397

Sammarco PW, Carleton JH (1982) Damselfish territoriality and coral community structure: reduced grazing and effects on coral spat. Proc 4th Intl Coral Reef Symp 2: 339-344

Sanchez JA (1995) Benthic communities and geomorphology of the Tesoro Island coral reef, Colombian Caribbean. An Inst Invest Mar Punta Betin 24: 55-77

Sandía J, Medina R (1987) Aspectos de la Dinámica Poblacional de *Acropora* cervicornis en el Parque Nacional Archipiélago de Los Roques. Tesis de Grado, Escuela de Biología, Universidad Central de Venezuela, Caracas, Venezuela

Santavy DL, Peters EC (1997) Microbial pests: coral disease in the western Atlantic. Proc 8th Intl Coral Reef Symp: 607-612

Scatterday JW (1974) Reefs and associated coral assemblages off Bonaire, Netherlands Antilles, and their bearing on Pliestocene and Recent reef models. Proc 2nd Intl Coral Reef Symp 2: 85-106

Schumacher H, Plewka M (1981) The adaptive significance of mechanical properties versus morphological adjustments in skeletons of *Acropora palmata* and *Acropora cervicornis* (Cnidaria, Scleractinia). Proc 4th Int Coral Reef Symp 2: 121-128.

Schumacher H, Zibrowius H (1985) What is hermatypic? A redefinition of ecological groups in corals and other organisms. Coral Reefs 4:1–9

Shearer T, Oppen MV, Romano S, Worheide G (2002) Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). Molec Ecol 11: 2475-2487

Shinn EA (1963) Spur and groove formation on the Florida Reef Tract. J Sed Petr 33: 291-303

Shinn EA (1966) Coral growth-rate: An environmental indicator. J Paleont 40: 233-240

Shinn EA (1976) Coral reef recovery in Florida and the Persian Gulf. Environ Geol 1: 241-254

Shinn EA (1980) Geologic history of Grecian Rocks, Key Largo Reef marine Sanctuary. Bull Mar Sci 30: 646-656

Shinn EA, Hudson JH, Halley RB, Lidz B (1977) Topographic control and accumulation rate of some Holocene coral reefs: South Florida and Dry Tortugas. Proc 3rd Intl Coral Reef Symp 2: 1-7

Shinn EA, Hudson JL, Robbin DM, Lidz B (1981) Spurs and grooves revisited: Construction versus erosion Looe Key Reef, Florida. Proc 4th Intl Coral Reef Symp 1: 475-483

Shinn EA, Lidz BH, Halley RB, Hudson JH, Kindinger JL (1989) Reefs of Florida and the Dry Tortugas: Field Trip Guidebook T176, Am Geophys Union, Washington DC.

Shinn EA, Reich CD, Hickey TD, Lidz BH (2003) Staghorn tempestites in the Florida Keys. Coral Reefs 22: 91-97

Shinn EA, Smith GW, Prospero JM, Betzer P, Hayes ML, Garrison V, Barber RT (2000) African dust and the demise of Caribbean coral reefs. Geophy Res Lett 27: 3029-3032.

Shulman MJ (1984) Resource limitation and recruitment patterns in coral reef fish assemblages. J Exp Mar Biol Ecol 74: 85-109

Smith SH (1988) Cruise ships: a serious threat to coral reefs and associated organisms. Ocean Shoreline Mgmt 11: 231-248

Smith SR, Ogden JC (eds) (1994) Status and recent history of coral reefs at the CARICOMP network of Caribbean marine laboratories. In: Ginsberg RN (comp) Proceedings of the colloquium on global aspects of coral reefs: Health, hazards, and history. RSMAS-Univ Miami, FL p 73-79

Soong K (1991) Sexual reproductive patterns of shallow-water reef corals in Panama. Coral Reefs 49: 832–846

Soong K, Lang JC (1992) Reproductive integration in coral reefs. Biol Bull 183: 418-431

Starck WA III, Davis WP (1966) Night habits of fishes of Alligator Reef, Florida. Ichthyologica 4: 313-356

Stanley SM (1966) Paleoecology and diagenesis of Key Largo Limestone, Florida. Amer Assoc Petr Geol Bull 50: 1927-1947

Sterrer W (1986) Marine fauna and flora of Bermuda. A systematic guide to the identification of marine organisms. Wiley-Interscience, NY

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 Res Bull 131: 25

Stoddart DR (1974) Post-hurricane changes on the British Honduras reefs: Re-surveys of 1972. Proc 2nd Intl Coral Reef Symp 2: 473-483

Storr JF (1964) Ecology and oceanography of the coral-reef tract, Abaco Island, Bahamas. Geol Sco Amer Spec Pap 79, 98 p

Sullivan KM, Chiappone M, Lott C (1994) Abundance patterns of stony corals on platform margin reefs of the Caicos Bank. Bahamas J Sci 1: 2-11

Sumich, JL (1996) An Introduction to the Biology of Marine Life, 6th Ed. Wm. C. Brown Publishers, Boston, MA

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.* Env Microbiol 5:250-255.

Sutherland KP, Ritchie KB (2004) White pox disease of the Caribbean elkhorn coral, *Acropora palmata*. In: Rosenberg E, Loya Y (eds) Coral Health and Disease. Springer, Berlin p 289-300

Swanson DW, Chiappone M, Miller SL (in review) Coral disease prevalence in the Florida Keys National Marine Sanctuary. Mar Ecol Prog Ser

Szmant AM (1986) Reproductive ecology of Caribbean reef corals. Coral Reefs 5: 43 53

Szmant AM (2002) Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries 25: 743-766

Szmant AM, Forrester A (1996) Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. Coral Reefs 15: 21-41

Szmant AM, Miller MW (in press) 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. Proc 10th Intl Coral Reef Symp

Talge H (1990) Impact of recreational divers on coral reefs in the Florida Keys. Diving for Science 365-373

Talge H (1991) Impact of Recreational Divers on Scleractinian Corals of the Florida Keys. MS Thesis, Univ South Florida, Tampa, FL

Tarrant AM, Atkinson MJ, Atkinson s(2004) Effects of steroidal estrogens on coral growth and reproduction. Mar Ecol Prog Ser 269: 121-129

Thresher RE (1976) Field analysis of the territoriality of the three-spot damselfish, Eupomacentrus planifrons (Pomacentridae). Copeia 1976: 266-276

Tomascik T, Sander F (1987) Effects of eutrophication on reef-building corals. I. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. Mar Biol 94: 53-75

Tunnell JW (1988) Regional comparison of southwestern Gulf of Mexico to Caribbean Sea coral reefs. Proc 8th Intl Coral Reef Symp 3: 303-308

Tunnell JW (1992) Natural versus human impacts to southern Gulf of Mexico coral reef resources. Proc 7th Intl Coral Reef Symp 1: 300-306

Tunnicliffe V (1981) Breakage and propagation of the stony coral *Acropora* cervicornis. Proc Nat Acad Sci 78: 2427-2431

Tunnicliffe V (1983) Caribbean staghorn populations: Pre-hurricane Allen conditions in Discovery Bay, Jamaica. Bull Mar Sci 33: 132-151

Van Moorsel GWNM (1988) Early maximum growth of stony corals (Scleractinia) after settlement on artificial substrata on a Caribbean reef. Mar Ecol Prog Ser 50: 127-135

Van Oppen JM, Willis LB, Vugt WH, Miller JD (2000) Examination of species boundaries in the *Acropora cervicornis* group (Scleractinia, Cnidaria) using nuclear DNA sequence analyses. Mol Ecol 9: 1363-1373

Van Veghel MLJ, Hoetjes PC (1995) Effects of tropical storm Bret on Curaçao reefs. Bull Mar Sci 56: 692-694

Vargas-Angel B, Thomas JD, Hoke SM (2003) High-latitude *Acropora cervicornis* thickets off Fort Lauderdale, Florida, USA. Coral Reefs 22: 465-473

Vaughan TW (1915) The geological significance of the growth rate of the Floridian and Bahamian shoal-water corals. J. Wash. Acad. Sci. 5: 591-600

Vaughn TW, Wells JW (1943) Revision of the suborders, families and genera of the Scleractinia. Geol Soc Amer Spec Pap 44.

Verrill, AE (1902) Notes on the *genus Acropora* (*Madrepora* Lamarck) with descriptions and figures of types and several new species. Trans Conn Acad Arts Sci 11: 207-266

Veron JEN (1986) Corals of Australia and the Indo-Pacific. Australian Institute of Marine Science. Townsville: 644

Veron JEN (2000) Corals of the World. Australian Institute of Marine Science 1: 463

Veron JEN, Wallace CC (1984) Scleractinia of eastern Australia. Family Acroporidae. Australian Institute of Marine Science and James Cook University Vol. 6 (part 5): 485

Vollmer SV, Palumbi SR (2002) Hybbridization and the evolution of reef coral diversity. Science 296: 2023-2025

Wallace CC (1985) Four years of coral recruitment to five reef front sites. Proc 5th Intl Coral Reef Symp 4: 385-390

Wallace CC, Bull GD (1981) Patterns of juvenile coral recruitment on a reef front during a spring-summer spawning period. Proc 4th Intl Coral Reef Symp 2: 345-350

Wapnick CM, Precht WF, Aronson RB (2004) Millenial-scale dynamics of staghorn coral in Discovery Bay, Jamaica. Ecol Letters 7: 354-361

Ward S, Harrison P (2000) Changes in gametogenesis and fecundity of acroporid corals that were exposed to elevated nitrogen and phosphorus during the ENCORE experiment. J. Exp Mar Biol Ecol 246:179–221

Weil E (2004) Coral reef diseases in the wider Caribbean. In: Rosenberg E, Loya Y (eds) Coral Health and Disease. Springer, Berlin p 69-104

Weil E, Urreiztieta I, Garzón-Ferreira J (2002) Geographic variability in the incidence of coral and octocoral diseases in the wider Caribbean. Proc 9th Intl Coral Reef Symp 2:1231–1237

Wellington GM, Fitt WK (2003) Influence of UV radiation on the survival of larvae from broadcast-spawning reef corals. Mar Biol 143: 1185-1192

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

Wells JW, Lang JC (1973) Appendix. Systematic list of Jamaican shallow-water Scleractinia. Bull Mar Sci 23: 55-58

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Ann Rev Ecol Syst 15: 393-425

Wheaton JW, Jaap WC (1988) Corals and other prominent benthic cnidaria of Looe Key National Marine Sanctuary, FL. Fla Mar Res Publ 43

Wheeler AJ, Bett BJ, Billett DSM, Masson DG, Mayor D (2003) The impact of demersal trawling on NE Atlantic deep-water coral habitats: the Darwin Mounds, U.K. In: J. Thomas & P. Barnes (eds) Proceeding from the Symposium on the Effects of Fishing Activities on Benthic Habitats: Linking Geology, Biology, Socioeconomics and Management, American Fisheries Society, Bethesda, Maryland, USA.
Williams AH (1978) Ecology of three-spotted damselfish, social organization, age structure and population stability. J Exp Mar Biol Ecol 34: 197-214

Williams DE, Miller MW (in press) Photo-monitoring of *Acropora palmata* & *Acropora cervicornis* on Florida reefs: Importance of disease & predation to growth & survivorship. Proc 10th Intl Coral Reef Symp

Williams DE, Miller MW (In review) Coral disease outbreak: pattern, prevalence, and transmission. Mar Ecol Prog Ser

Williams EH, Bunkley-Williams L (1990) The world-wide coral reef bleaching cycle and related sources of coral mortality. Atoll Res Bull 335: 1-71

Woodley C, Bruckner A, Galloway S, McLaughlin S, Downs C, Fauth J, Shott E, Larkin K (2003) "Coral Disease and Health: A National Research Plan" NOAA, Silver Spring MD 66pp.

Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Land JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe VJ, Wahle CM, Wulff JL, Curtis ASC, Dallmeyer MD, Jupp BP, Koehl MAR, Niegel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. Science 214: 749-755

Zea S, Duque Tobon F (1989) Bleaching of reef organisms in the Santa Marta region, Colombia: 1987

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 Res Bull 456: 30

Zlatarski VN, Estalella NM (1982) Les scleractiniaires de Cuba avec des donnees sur les organisms associes. Acad Bulgare des Sciences, Sofia Bulgaria

Appendix A: Current and historic management

In order to assess the adequacy of current management measures (i.e., the fourth ESA listing factor) that could prevent further decline of *Acropora palmata* and *A. cervicornis*, the BRT researched and summarized, by authority, existing regulatory mechanisms that afford protection to corals. In most cases, management actions were aimed at protecting coral or coral reefs in general and did not specifically mention *Acropora* spp. A brief summary of management measures within the U.S. and foreign jurisdictions follows.

1 Federal

1.1 Fisheries Management Councils and Fisheries Management Plans

South Atlantic Fishery Management Council

The jurisdiction of the South Atlantic Fishery Management Council (SAFMC) includes federal waters off the states of North Carolina, South Carolina, Georgia, and Florida. Significant *Acropora* populations are distributed in federal waters off the southeastern coast of Florida. These occur primarily within the boundaries and jurisdiction of the Florida Keys National Marine Sanctuary (FKNMS), which was designated in 1990, but also include Biscayne National Park southeast of Miami and Dry Tortugas National Park west of Key West. The FKNMS management plan was implemented in 1997 after being designated in 1990.

The SAFMC is in the process of developing ecosystem-based management in lieu of individual single-species or multispecies fishery management plans, and released an action plan in August 2004 titled "Ecosystem-based Management: Evolution from the Habitat Plan to a Fishery Ecosystem Plan" (http://ocean.floridamarine.org/efh_coral/pdfs/saecoationplanaug04.pdf). This plan is founded upon three broad actions:

1. Adoption of a proactive approach to protect and enhance Essential Fish Habitat for all managed species.
2. Adoption of precautionary and proactive management plans.
3. Pioneering application of an ecosystem-based approach to fisheries management.

Workshops were held in 2003 and 2004 and will continue during 2005 to help develop the improved understanding required for the transition from single-species to ecosystem-based management. Identification of Coral Habitat Areas of Particular Concern (HAPC) is identified in the action plan as part of this process. However, as noted above, significant *Acropora* populations lie within the jurisdiction of the FKNMS rather than the SAFMC in the southeastern U.S.

Gulf of Mexico Fishery Management Council

The Gulf of Mexico Fishery Management Council (GMFMC) includes federal waters from Texas to the west coast of Florida. Some colonies of *Acropora* occur in the Tortugas region on banks outside of the FKNMS and elsewhere in the region. Any such colonies would be of considerable scientific interest, as is the case for the single-known *A. palmata* colony that occurs at a depth of over 20 m within the Flower Garden Banks National Marine Sanctuary.

The Coral-Coral Reef Fishery Management Plan (under the Magnusen-Stevens Act, see below) was developed by the Gulf of Mexico and the South Atlantic Fishery Management Councils and enacted in April 1982. The management councils have jurisdiction from North Carolina to the U.S.- Mexico Border. The management unit includes all of the corals and coral reefs in the Fishery Conservation Zone. The FMP identified the problems with corals conservations as: degradation from natural and man-made impacts; limited information on many of the species; susceptibility to stresses due to the northern location of the resources; complex and contradictory management objectives; poor public knowledge of the importance of corals and reefs; and poor enforcement of existing laws and regulations.

All of the stony corals (Scleractinia, Milleporina) and the gorgonian sea fan (*Gorgonia*) are protected from harvest, sale, and destruction on the seabed in U.S. Federal waters. Note that the coral FMP can only regulate fishing related activities: a non-fishing activity that destroys corals is exempt from coral FMP regulation. Special managed areas (Habitat Area of Particular Concern, HAPC) were established on the Florida Middle Grounds, East and West Flower Garden Banks, Gray's Reef, and the Oculina Banks off central eastern Florida. Subsequently, other HAPCs have been recommended by the GMFMC to the Department of Commerce (NOAA) for approval including Pulley Ridge off southwest Florida and the Stetson, McGrail, Bright, Geyer, and Sonnier Banks in the northwestern Gulf of Mexico. There are no specific management measures for *Acropora* spp. in the coral FMP.

Caribbean Fishery Management Council

The Caribbean Fishery Management Council developed a Fishery Management Plan, Regulatory Impact Review, and Final EIS for corals and reef-associated plants and invertebrates of Puerto Rico and the U.S. Virgin Islands (U.S.V.I.) in 1994. This FMP provides protection in the form of no-harvest for Exclusive Economic Zone portions of the insular shelves of Puerto Rico and the U.S.V.I. for all coral species. This alternative was selected due to the lack of biological information necessary to estimate a Maximum Sustainable Yield for the species, coupled with the extremely slow growth rates for most corals. In the case of the U.S.V.I., the EEZ starts at 3.0 nautical miles (nmi) from shore and in Puerto Rico, the EEZ starts at 10.2 nmi. With the possible exception of some *Acropora cervicornis* in the very limited shallower portions of the EEZ (e.g., Lang Bank, St. Croix), this FMP has little effect on acroporid corals.

1.2 Executive Orders and Acts

Executive Order 13089, "Coral Reef Protection

Executive Order 13089, "Coral Reef Protection" (www.coralreef.gov/execorder.cfm), issued by President William J. Clinton on 11 June 1998, established the U.S. Coral Reef Task Force (USCRTF) with a central goal of preserving and protecting the biodiversity, health, heritage, and social and economic value of U.S. coral reef ecosystems and the marine environment. In 2000, the USCRTF published "The National Action Plan to Conserve Coral Reefs" (http://www.coralreef.gov/CRTFAxnPlan9.pdf), which identified two fundamental themes for immediate and sustained national action: 1) understand coral reef ecosystems and the natural and anthropogenic processes that determine their health and viability and 2) quickly reduce the adverse impacts of human activities on coral reefs and associated ecosystems. The action plan identified marine protected areas (MPAs) as a promising conservation tool and proposed a critical conservation goal for MPAs in the U.S. that included: 1) strengthening protection within existing MPAs; 2) establishment of no-take ecological reserves with a goal of 20% of all representative U.S. coral reefs and associated habitats by 2010; 3) a national assessment of the remaining gaps in coverage; and 4) strengthened support for international cooperation to conserve global biodiversity. The USCRTF does not identify *Acropora* for directed conservation and protective actions, but is implementing programs and projects to help protect and conserve entire coral reef ecosystems.

Coral Reef Conservation Act of 2000

The Coral Reef Conservation Act (CRCCA) (16 U.S.C. 6401 et seq.) was passed in 2000. The CRCCA recognizes the unique nature of coral reef communities and has three main goals:

1. The creation of a National Coral Reef Action Strategy;
2. The financial promotion of governmental, educational, and non-governmental conservation programs; and
3. Granting of additional power to the Secretary of Commerce to protect coral reef ecosystems.

The CRCCA charges NOAA with the development and periodic review of a National Coral Reef Action Strategy that addresses sustainable uses, monitoring, mapping, and public education of coral reef resources. Under the CRCCA, NOAA can provide grants to governmental, education, and non-governmental entities with expertise in coral reef conservation, and to fund monitoring, mapping, and education programs of coral reefs.

The National Marine Sanctuaries Act of 1972

This Act authorizes the Secretary of Commerce, with significant public input, to designate and manage national marine sanctuaries based on specific standards. It provides for supervision by the Secretary over any permitted private or federal action that is likely to destroy or injure a sanctuary resource, and requires periodic evaluation of implementation of management plans and goals for each sanctuary. The Act also specifies prohibited activities, penalties and enforcement.

The Act prohibits the following activities: destroying, causing the loss of, injuring a sanctuary resource managed under law or regulations for that sanctuary; possessing, selling, delivering, carrying, transporting, or shipping a sanctuary resource taken in violation of the Act; interfering with enforcement of the Act; and violating a provision of the Act or regulations of permits issued under it. Furthermore, the Secretary must conduct enforcement activities to carry out the Act. A person authorized to enforce the Act may board, search, inspect or seize a vessel, equipment, stores and cargo suspected of being used to violate the Act, and seize unlawfully taken sanctuary resources. The Act requires the Secretary to promote the use of national marine sanctuaries for research, monitoring, evaluation and educational programs as are necessary and reasonable to carryout the purposes and policies of the Act.

Continental Shelf Act

Outer Continental Shelf Lands Act (CSA) of 1953 (43 U.S.C. 1331 - 1356, P.L. 212, Ch. 345, August 7, 1953, 67 Stat. 462) as amended by P.L. 93-627, January 3, 1975, 88 Stat. 2130; P.L. 95-372, September 18, 1978, 92 Stat. 629; and P.L. 98-498, October 19, 1984, 98 Stat. 2296.

The 1953 statute defines the Outer Continental Shelf (OCS) as all submerged lands lying seaward of State coastal waters (3 miles offshore) which are under U.S. jurisdiction. The statute authorized the Secretary of Interior to promulgate regulations to lease the OCS in an effort to prevent waste and conserve natural resources, as well as to grant leases to the highest responsible qualified bidder as determined by competitive bidding procedures.

The Deepwater Port Act of 1974 (P.L. 93-627) authorizes the Secretary of Transportation, after consultation with the Secretary of Interior, to waive the removal requirements for a deepwater port if its components can be used in conjunction with a mineral lease sale.

Numerous amendments were incorporated in the Outer Continental Shelf Lands Act amendments of 1978 (P.L. 95-372). Title II of these amendments provides for the cancellation of leases or permits if continued activity is likely to cause serious harm to life, including fish and other aquatic life. It also stipulates that economic, social, and environmental values of the renewable and nonrenewable resources are to be considered in management of the OCS.

The timing and location of leasing activities are to be based on several factors, including the relative environmental sensitivity and marine productivity of different areas of the OCS. An environmental studies program is authorized and the Secretary of the Interior is required to study any region included in a lease sale in order to assess and manage environmental impacts on the OCS.

Title III of these amendments established an Offshore Oil Spill Pollution Compensation Fund to be financed by a tax on oil obtained from the OCS and stipulated the damages for which claims could be made against the fund.

Title IV of the amendments established a Fishermen's Contingency Fund to compensate fishermen for damages of fishing gear by materials, equipment, tools, containers, or other items associated with oil and gas exploration.

Title V amended the 1972 Coastal Zone Management Act (CZMZ) to authorize grants to coastal states under a Coastal Energy Impact Program.

Amendments enacted in 1984 provided for changes to certain administrative provisions in the Fishermen's Contingency Fund.

In 1974, the tramp freighter *Lola*, struck and grounded on Looe Key Reef, Florida. The Supreme Court had recently rendered State jurisdictional sovereignty at three nautical miles from the nearest landfall. As such, the incident at Looe Key was beyond the state of Florida's jurisdiction. The U.S. Fish and Wildlife Service investigated the incident and held the ship responsible under a claim that the CSA applied to the incident. The Circuit Court of Appeals ruled that the CSA did not apply to natural resource injuries.

Magnusen-Stevens Act

The 1996 amendments to the Magnuson-Stevens Fishery Conservation and Management Act (Magnuson-Stevens Act) set forth a new mandate for the National Marine Fisheries Service (NMFS), regional fishery management councils (FMC), and other Federal agencies to identify and protect important marine and anadromous fish habitat. The Essential Fish Habitat (EFH) provisions of the Magnuson-Stevens Act support one of the Nation's overall marine resource management goals - maintaining sustainable fisheries. Essential to achieving this goal is the maintenance of suitable marine fishery habitat quality and quantity. The FMCs, with assistance from NMFS, have delineated "essential fish habitat" (EFH) for Federally managed species, including corals and coral reefs. Federal action agencies which fund, permit, or carry out activities that may adversely affect EFH are required to consult with NMFS regarding the potential impacts of their actions on EFH, and respond in writing to NMFS or FMC recommendations. In addition, NMFS and the FMCs may comment on and make recommendations to any state agency on their activities that may affect EFH. Measures recommended by NMFS or an FMC to protect EFH are advisory, not proscriptive.

Coastal Zone Management Act of 1972

The federal Coastal Zone Management Act (CZMA) of 1972 encourages coastal states to develop comprehensive management programs that ensure the beneficial use, protection and management of the Nation's coastal resources. To encourage the adoption and implementation of these management programs, coastal states whose programs receive approval from the U.S. Department of Commerce, National Oceanic and Atmospheric Administration (NOAA) are empowered to review federal activities that affect the state's approved management program (www.coastalmanagement.noaa.gov/czm). This authority to review federal activities is called "federal consistency." The process allows states to review the following activities for compliance with their approved management program:

1. Activities conducted by or on behalf of a federal government agency;
2. Federally funded activities;
3. Activities that require a federal license or permit; and

4. Activities conducted pursuant to the Outer Continental Shelf Lands Act minerals exploration plan or lease.

If a state with an approved management program determines that a proposed federal activity is “inconsistent” with the requirements of the state’s approved program, the applicant/federal agency is prohibited from conducting the activity.

Table A-1. Summary of states within the geographic range of Atlantic acroporids with federally approved Coastal Management Programs (CMP) enacted pursuant to the Coastal Zone Management Act. URL = internet location where the CMP can be found.

State	Year CMP signed	URL
Florida	**1981**	www.dep.state.fl.us/cmp
Puerto Rico	1978	www.coralpr.net www.gobierno.pr/drna
Virgin Islands	1979	www.viczmp.com

In an effort to develop a more comprehensive solution to the problem of polluted runoff in coastal areas, the U.S. Congress expanded the CZMA in 1990 to include a new section 6217 entitled "Protecting Coastal Waters". Section 6217 requires that states with approved coastal zone management programs develop Coastal Nonpoint Pollution Programs wherein state programs incorporate management measures to address land-based sources of run-off from agriculture, forestry, urban development, marinas, hydromodification (e.g., stream channelization), and the loss of wetlands and riparian areas. In keeping with the successful state-federal partnership to manage and protect coastal resources achieved by the CZMA, section 6217 envisioned that nonpoint source programs developed under section 319 of the Clean Water Act (CWA) would be combined with existing coastal management programs. By combining the water quality expertise of state 319 agencies with the land management expertise of coastal zone agencies, section 6217 was designed to more effectively manage nonpoint source pollution in coastal areas. To facilitate development of state coastal nonpoint programs and ensure coordination between states, administration of section 6217 at the federal level was assigned to NOAA and the Environmental Protection Agency. Both Puerto Rico and the U.S.V.I. have fully approved nonpoint programs; Florida has a few conditions remaining prior to approval.

The Rivers and Harbors Act of 1899

The Federal government has two long-standing programs that regulate various activities in wetlands and other water bodies. Both of these regulatory programs require permits for activities that could adversely impact corals and other aquatic species. The authority for these regulatory programs is derived from two statutes:

1. The Rivers and Harbor Act of 1899 (RHA), 33 U.S.C. §401-413 (1982); and
2. The Clean Water Act (CWA), 33 U.S.C. §1251-1376 (1982).

The main purpose of the RHA is to protect navigation in navigable waters of the U.S. This regulatory program requires a permit from the U.S. Army Corps of Engineers

(Corps) to perform a variety of activities, including dredging, filling, or placement of structures, in navigable waters. Permit applications are evaluated for their impedance to navigation. However, dredging and filling activities that impede navigation can also adversely affect aquatic organisms, including corals.

The Corps has defined "navigable waters of the Unites States" to include:

1. All intrastate waterways capable of carrying interstate commerce (33 C.F.R. §329.9;
2. Artificially created water bodies, including canals (33 C.F.R.§ 329.8 (a));
3. Inland marina basins (Kaiser Aetna v. Unites States, 444 U.S. 164 (1979); and
4. Formally navigable waters (33 C.F.R. §329.7).

Determinations of navigability may be obtained from 33 C.F.R. §329.14 and the lists of all water bodies that have been determined to be navigable are maintained at each Corps District Office. Once it has been determined that a water body is navigable under the RHA, jurisdiction extends to the "edge" of the water body. For rivers and lakes, RHA jurisdiction extends to the ordinary high water mark that is determined by a procedure set forth in 33 C.F.R. §329.11 (a) (1). For oceanic and tidal waters, RHA jurisdiction extends to the mean high water line that is established by utilizing available tidal data. Where precise location of the jurisdictional limit is required, the mean high water line is established by averaging tidal data for a period of 18.6 years (33 C.F.R. §329.12). Marshlands and similar areas are considered navigable, and jurisdiction extends only so far as the area is subject to inundation (33 C.F.R. §329.11(2)).

Section 9 of the RHA (33 U.S.C. § 401) prohibits the construction of bridges, causeways, dams, or dikes over any navigable water of the United States without (1) consent of Congress, or (2) consent of the State legislature for any navigable water wholly within the limits of one State. In addition, a permit must be obtained from the U.S. Coast Guard for bridges and causeways, and from the Corps for dams and dikes (bridges and causeways 33 C.F.R. §114.01 *et seq.*; dams and dikes (33 C.F.R. §321 *et seq.*).

Section 10 of the RHA prohibits any unauthorized obstruction of the navigability of any waters of the U.S. and prohibits dredging or filling in navigable waters without the approval of the Corps. Permits are required under this section for wharfs, piers, breakwaters, jetties, and other obstructions to the "navigable capacity" of waters, and for activities that may "alter or modify the course, location, condition, or capacity" of any navigable water. Section 10 has consistently been given a broad interpretation by the Courts. Two examples of court rulings that show broad interpretation of what constitutes a dredging and/or filling activity include:

1. United States v. M.C.C. of Florida, Inc. (772 F.2d 1501 (11th Cir. 1985)) found that repeated trips by tugboats in shallow waters constituted illegal dredging and filling under Section 10.

2. United States v. Republic Steel Corp. (362 U.S. 432 (1960) determined that discharges of industrial wastes that progressively decrease the depth of a water body constituted prohibited obstruction covered by Section 10.

The Clean Water Act of 1987

Section 404 Program

The 1977 amendments to the Federal Water Pollution Control Act of 1948 and 1972 (PL 92-500) are commonly known as the Clean Water Act (CWA) (due to a parenthetical revision in Section 518). Congress stated that the objective of the CWA was to "restore and maintain the chemical, physical, and biological integrity of the Nation's waters" (33 U.S.C. §1251(A). Section 404 (a) of the CWA gives the authority to the Secretary of the Army (through the Corps) to issue permits, after notice and opportunity for public hearings, for the discharge of dredged or fill material into navigable waters at specified disposal sites. Section 404 (b) states that disposal sites shall be specified through the application of guidelines developed by the Administrator of the U.S. Environmental Protection Agency (USEPA), in conjunction with the Secretary. These "Guidelines for Specification of Disposal Sites for Dredged or Fill Material" (40 CFR 230) have become known as the "Section 404 (b)(1) Guidelines" (Guidelines); these were finalized on December 24, 1980, and remain in effect. Section 404 (c) authorizes the USEPA to prohibit (veto) any defined areas as a disposal site if it is determined that discharges of materials into such areas will have "an unacceptable adverse effect on municipal water supplies, shellfish beds and fisheries areas (including spawning and breeding areas), wildlife, or recreational areas." Issuance of a Section 404 permit requires water quality certification by the appropriate State agency (33 U.S.C.1341, Section 401).

The CWA limits federal jurisdiction to "navigable waters," which it defines as "waters of the United States" (33 U.S.C. §1362(7)). The Corps' regulations (33 CFR 328 (a)) and the Section 404 (b)(1) Guidelines (40 CFR 230.3 (s)) define "waters of the United States to include seven categories:

1. All waters which are currently used, or were used in the past, or may be susceptible to use in interstate or foreign commerce, including all waters which are subject to the ebb and flow of the tide;
2. All interstate waters including interstate wetlands;
3. All other waters such as intrastate lakes, rivers, streams (including intermittent streams), mudflats, sandflats, wetlands, slough, prairie potholes, wet meadows, playa lakes, or natural ponds, the use, degradation or destruction of which could affect interstate or foreign commerce including and such waters:
    a. which are or could be used by interstate of foreign travelers for recreational or other purposes; or
    b. which fish or shellfish are or could be taken and sold in interstate or foreign commerce; or
    c. which are used or could be used for industrial purpose by industries in interstate commerce.
4. All impoundments of waters otherwise defined as waters of the United States under the definition;

5. Tributaries of waters identified in paragraphs 1-4 of this section;
6. The territorial sea;
7. Wetlands adjacent to waters (other than waters that are themselves wetlands) identified in paragraphs 1-6 of this section; waste treatment systems, including treatment ponds or lagoons designed to meet the requirements of CWA (other than cooling ponds as defined in 40 CFR §423.11(m)) which also meet the criteria of this definition) are not waters of the United States.

The purpose of the Section 404 (b)(1) Guidelines is to restore and maintain the chemical, physical, and biological integrity of waters of the U.S. through the control of discharges of dredged or fill material (40 CFR 230.1). Fundamental to the Guidelines is the precept that dredged or fill material should not be discharged into the aquatic ecosystem, "unless it can be demonstrated that such a discharge will not have an unacceptable adverse impact either individually or in combination with known and/or probable impacts of other activities affecting the ecosystems of concern." The Guidelines further state that "From a national perspective, the degradation or destruction of special aquatic sites, such as filling operations in wetlands, is considered to be among the most severe environmental impacts covered by these Guidelines. The guiding principle should be that degradation or destruction of special sites may represent an irreversible loss of valuable aquatic resources."

Special aquatic sites are defined as geographical areas, large or small, possessing special ecological characteristics of productivity, habitat, wildlife protection, or other important and easily disrupted ecological values (40 CFR 230 Subpart E). These areas are generally recognized as significantly influencing or positively contributing to the general overall environmental health or vitality of the entire ecosystem of a region. The Guidelines lists the following communities to represent "Special Aquatic Sites": sanctuaries and refuges; wetlands; mudflats; vegetated shallows; coral reefs; riffle and pool complexes. Thus, coral reefs, including *Acropora* spp., are afforded special protection under the Guidelines.

Dredging and filling activities can adversely affect colonies of reef-building organisms by burying them, by releasing contaminants, such as hydrocarbons into the water column, by reducing light penetration through the water, and by increasing the level of suspended particles in the water column. The Guidelines recognize that coral organisms are "extremely sensitive to even slight reductions in light penetration or increases in suspended particulates." These adverse effects will cause a loss of productive colonies that in turn provide habitat for many species of highly specialized aquatic organisms.

Advanced Identification of Disposal Areas under Section 404

A potential mechanism for providing additional protection to coral communities is through the use of Advanced Identification of Disposal Areas (ADID) (40 CFR 230.80). Under this action, the USEPA and the permitting authority, (e.g., the Corps or State in the case of a state-delegated program) on their own initiative or at the request of any other party after consultation with any affected State that is not the permitting authority, may identify sites which are considered as:

1. Possible future disposal sites, including existing disposal sites and non-sensitive areas; or
2. Areas generally unsuitable for disposal site specification.

To provide the basis for ADID of disposal areas and areas unsuitable for disposal, the USEPA and the permitting authority shall consider the likelihood that use of the area in question for dredge or fill material disposal will comply with the Guidelines. Thus, it is possible that coral reef sites, including sites dominated by *Acropora* spp. may be determined through the ADID process as areas generally unsuitable for disposal of dredged or fill material.

In Florida, ADIDS have been developed for western Biscayne Bay (Cutler Ridge), the Florida Keys, the Loxahatchee River, Eastern Everglades, and Rookery Bay. The use of ADID can help applicants identify areas where permitting difficulties can be expected. As far as we can determine, this level of protection has not been applied to any coral sites nationally.

1.3 National Parks, Reserves, Sanctuaries

In 1916 President Woodrow Wilson approved legislation creating the National Park Service within the Interior Department. The act made the bureau responsible for Interior's national parks and monuments. In managing these areas, the Park Service was directed "to conserve the scenery and the national and historic objects and the wild life therein and to provide for the enjoyment of the same in such a manner and by such means as will leave them unimpaired for the enjoyment of future generations."

The John Pennekamp Coral Reef State Park was established in 1960 as the first coral reef MPA worldwide (see 5.2.1). Three National Parks have been designated in the south Florida marine environments. Two of these, Dry Tortugas (DTNP; 1992) and Biscayne National Parks (BNP; 1980), include significant coral reefs. Prior to the establishment of DTNP, the Fort Jefferson National Monument (1935) protected part of the Tortugas region, specifically the fort, the islands, and the seabed out to approximately 20 m depth. In addition, Everglades National Park (1947) includes much of Florida Bay, an important subtropical lagoon with vital ecological connections with the Florida Reef Tract.

Navassa is a small (~5 km^2) uninhabited island approximately 40 miles off the southwest coast of Haiti. Claimed by the U.S. in 1857 under the Guano Act, the island is currently under jurisdiction of the U.S. National Wildlife Refuge system. Because the island is uninhabited, there is no local jurisdiction due to its remoteness and international complications, active management and/or enforcement is lacking. Populations of *Acropora palmata* are expanding around the island, while *A. cervicornis* is extremely rare and in poor condition (Miller 2003).

The USFWS manages several large *National Wildlife Refuges* that protect extensive areas of shallow hardbottom and seagrass environments in the lower Florida Keys, which also have important ecological connections with the Florida Reef Tract. Additional MPAs are managed by the State of Florida.

The National Marine Sanctuary Program (NOAA) has managed segments of the Florida Reef Tract since 1975. *The Key Largo National Marine Sanctuary* (1975) was established to protect 353 km^2 (103 nmi^2) of coral reef habitat offshore of the upper Florida Keys adjacent to John Pennekamp Coral Reef State Park. In 1981, the 18-km^2 (5.3-nm^2) *Looe Key National Marine Sanctuary* was established to protect the heavily used Looe Key Reef in the lower Florida Keys. These two national marine sanctuaries were, and continue to be, managed very intensively in terms of mooring buoy installation and maintenance, on-site enforcement and outreach programs, and scientific investigations.

By the late 1980s it had become evident that a broader, more holistic approach to protecting and conserving the health of coral reef resources in the Florida Keys had to be implemented. Irrespective of the intense management of small areas of the Florida reef tract, sanctuary managers were witnessing declines in water quality and the health of corals that apparently had a wide range of sources. The most obvious causes of decline were non-point-source discharges, habitat degradation from coastal development and resource over-use, and changes in reef fish populations because of over-fishing. Besides these factors, a main impetus for the establishment of the FKNMS were back-to-back-to-back major vessel groundings that severely damaged some offshore reef areas.

The threat of oil drilling in the mid to late 1980s off the Florida Keys, combined with reports of deteriorating water quality throughout the region (Kruczynski and McManus 2002, Leichter et al. 2003), occurred at the same time scientists were assessing adverse affects of coral bleaching, especially after the 1987 El Niño event (Glynn 1993), the 1983-84 Caribbean-wide mass mortality of the long-spined urchin (Lessios 1988), loss of living coral cover on reefs (Dustan and Halas 1987, Porter and Meier 1992), a major seagrass die-off in Florida Bay (Robblee et al. 1991), declines in reef fish populations (Ault et al. 1998), and the spread of coral diseases (Porter et al. 2001). These were topics of major scientific concern and the focus of several scientific workshops (e.g., Ginsburg 1994).

In the fall of 1989, subsequent to the catastrophic Exxon Valdez oil spill in Alaska, three large ships ran aground on the Florida Reef Tract within a brief, 18-day period. This final physical impact to the offshore reef tract, in conjunction with the cumulative effects of environmental degradation, prompted Congress to take action to protect the unique coral reef ecosystem of the Florida Keys. In November 1990, President Bush signed into law the Florida Keys National Marine Sanctuary and Protection Act (FKNMS Act).

The FKNMS Act designated 9,515 km^2 (2,774 nm^2) of coastal waters surrounding the Florida Keys as the *Florida Keys National Marine Sanctuary* and addressed two major concerns. First, there was an immediate prohibition on oil drilling, including mineral and hydrocarbon leasing, exploration, development, or production within the Sanctuary. In addition, the legislation prohibited the operation of vessels longer than 50 m (164 ft) in an internationally recognized “Area To Be Avoided” within and near the boundary of the Sanctuary.

Corals in general are afforded a number of mechanisms of protection under the various Action Plans that comprise the FKNMS Management Plan, but there are no particular programs for *Acropora* spp. In practice, however, *Acropora* spp. receive particular attention in the form of tight restrictions on the collection of samples for research and for restoration after damage from boat groundings and other sources of physical impacts.

Virgin Islands Coral Reef National Monument (VICRNM) was recently created and Buck Island Reef National Monument (BIRNM) was recently expanded by the designation of thousands of acres of non-extractive zones (2000 Executive Order). These new and expanded National Monument designations afford total protection to 7% of the St. Croix shelf and 3% of the St. John/St. Thomas shelf.

Florida Keys National Marine Sanctuaries and Protection Act of 1990

The Florida Keys National Marine Sanctuaries and Protection Act (FKNMSPA) (P.L. 101-605) was signed into law on November 16, 1990. The FKNMSPA places strict limits on operation of ships and prohibits the leasing, exploration, development, or production of minerals or hydrocarbons within the Florida Keys National Marine Sanctuary (FKNMS). The Act also directed the Secretary of Commerce (NOAA) to develop a comprehensive management plan and regulations for the Florida Keys National Marine Sanctuary pursuant to Sections 303 and 304 of the National Marine Sanctuaries Act (NMSA) (16 U.S.C. 1431 *et seq.*). The NMSA authorizes the development of management plans and regulations for national marine sanctuaries to protect their conservation, recreational, ecological, historical, research, educational, or aesthetic qualities.

The Final Rule to implement the comprehensive management plan for the FKNMS became effective on July 1, 1997. The Final Rule authorizes the Sanctuary to regulate activities “affecting the resources of the Sanctuary or any of the qualities, values, or purposes for which the Sanctuary is designated, in order to protect, preserve and manage the conservation, ecological, historical, and aesthetic resources and qualities of the area. In particular, the regulations are intended “to protect, restore, and enhance the living resources of the Sanctuary, to contribute to the maintenance of natural assemblages of living resources for further generations, to provide places for species dependent on such living resources to survive and propagate, to facilitate to the extent compatible with the primary objective of resource protection all public and private uses of the resources of the Sanctuary not prohibited pursuant to other authorities, to reduce conflicts between such compatible uses, and to achieve the other policies and purposes of the FKNMSPA.”

The Final Rule lists the following activities to be prohibited in the FKNMS:

1. Mineral and hydrocarbon exploration, development and production;

2. Removal of, or injury to, or possession of coral or live rock;
3. Alteration or, or construction on the seabed, except as an incidental result of anchoring, traditional fishing activities not prohibited, installation and maintenance of navigational aids, harbor maintenance, and construction, repair, replacement, or rehabilitation of docks, seawalls, breakwaters, piers, or marinas with less than ten slips that receive valid leases or permits;
4. Discharging or depositing of materials or other matter;
5. Operating a vessel in such a manner as to strike or otherwise injure coral, seagrass, or any other immobile organism attached to the seabed;
6. Diving or snorkeling without a flag;
7. The release of exotic species;
8. Damaging or removing markers;
9. Movement of, removal of, or injury to, or possession of Sanctuary historical resources;
10. Taking or possessing protected wildlife;
11. Possession or use of explosives of electrical charges;
12. Harvesting or possessing any marine life species, or part thereof, except in accordance with pertinent regulations of the Florida Administrative Code (46-42.001 through 46-42.003, 46-42.0035, 46-42.004 through 46-42.007, and 46-42.009), and
13. Interference with law enforcement.

Virgin Islands National Park (VINP)

The VINP was established on St. John, U S Virgin Islands in 1956 (16 USC Sec. 398). Marine portions surrounding St. John were added in 1962 (76 Stat. 746) and include 5,650 acres of water. Interpretation of recent aerial photographs (1999) shows the VINP marine environment consist of 28% unknown (areas deeper than 20 m), 34% coral reef and colonized hard-bottom, 20% submerged aquatic vegetation, and 17% sand (NOAA, 2001). Numerous shallow *Acropora* reefs occur in the park with regulations prohibiting the taking or harming of any corals. Moorings are provided for vessels to prevent damage to coral reef and hard-bottom habitats.

Virgin Islands Coral Reef National Monument (VICRNM)

The VICRNM was created by Presidential Proclamation under the Antiquities Act on 17 January 2001. It includes approximately 12,708 acres of submerged lands. The proclamation and draft interim regulations prohibit anchoring, except under emergency situations, and the harvest of any marine life with the exception of Blue Runner (a migratory coastal pelagic fish) off the southern coast of St. John and baitfish in Hurricane Hole. Only one area within VICRNM has any *Acropora* (Turner Point), as the waters of the national monument are too deep for these species. VICRNM effectively protects approximately 3% of the St. Thomas/St. John insular shelf above 100 fathoms (600 ft) in depth.

Buck Island Reef National Monument (BIRNM)

The BIRNM was expanded to approximately 18,000 acres through Presidential Proclamation under the Antiquities Act on 17 January 2001. The proclamation and draft interim regulations prohibit anchoring, except in an area of deep sand off the west end of the island, and the harvest of any marine life. Buck Island is known for its *Acropora* reefs that were virtually eliminated by the white band epizootic in the 1970s (Gladfelter 1982). Presently, *Acropora* spp. are showing some signs of recruitment and some regrowth of *A. palmata* was indicated in summer 2004 surveys. The expanded BIRNM effectively protects approximately 7% of the St. Croix insular shelf above 100 fathoms (600 ft) in depth.

ESA Candidate Species/Species of Concern
Both the staghorn and elkhorn corals are included on NOAA's candidate species list (see section 2.1.1). Species on this list do not receive any protection under the ESA; rather their inclusion is to primarily highlight species at risk, and to seek additional data regarding distribution and abundance.

2 State/Local

2.1 Florida

Florida Statute 253.001 - Board of Trustees of the Internal Improvement Trust Fund; duty to hold lands in trust
The existence of the Board of Trustees of the Internal Improvement Trust Fund is reaffirmed. All lands held in the name of the board of trustees shall continue to be held in trust for the use and benefit of the people of the state pursuant to s. 7, Art. II, and s. 11, Art. X of the State Constitution

Florida Statute 253.04 - Duty of board to protect, etc., state lands; state may join in any action brought
(1) The Board of Trustees of the Internal Improvement Trust Fund may police; protect; conserve; improve; and prevent trespass, damage, or depredation upon the lands and the products thereof, on or under the same, owned by the state as set forth in s. 253.03. The board may bring in the name of the board all suits in ejectment, suits for damage, and suits in trespass which in the judgment of the board may be necessary to the full protection and conservation of such lands, or it may take such other action or do such other things as may in its judgment be necessary for the full protection and conservation of such lands; and the state may join with the board in any action or suit, or take part in any proceeding, when it may deem necessary, in the name of this state through the Department of Legal Affairs.
(2) In lieu of seeking monetary damages pursuant to subsection (1) against any person or the agent of any person who has been found to have willfully damaged lands of the state, the ownership or boundaries of which have been established by the state, to have willfully damaged or removed products thereof in violation of state or federal law, to have knowingly refused to comply with or willfully violated the provisions of this chapter, or to have failed to comply with an order of the board to remove or alter any structure or vessel that is not in compliance with applicable rules or with conditions of authorization to locate such a structure or vessel on state-owned land, the board may

impose a fine for each offense in an amount up to $10,000 to be fixed by rule and imposed and collected by the board in accordance with the provisions of chapter 120. Each day during any portion of which such violation occurs constitutes a separate offense. This subsection does not apply to any act or omission which is currently subject to litigation wherein the state or any agency of the state is a party as of October 1, 1984, or to any person who holds such lands under color of title. Nothing contained herein impairs the rights of any person to obtain a judicial determination in a court of competent jurisdiction of such person's interest in lands that are the subject of a claim or proceeding by the department under this subsection.

(3) The Department of Environmental Protection is authorized to develop by rule a schedule for the assessment of civil penalties for damage to coral reefs in state waters. The highest penalty shall not exceed $1,000 per square meter of reef area damaged. The schedule may include additional penalties for aggravating circumstances, not to exceed $250,000 per occurrence. A determination of aggravating circumstances shall be based on factors relating to the cause of the damage such as, but not limited to:

(a) Absence of extenuating circumstances, such as weather conditions or other factors beyond the control of the vessel operator.
(b) Disregard for safe boating practices.
(c) Whether the vessel operator was under the influence of alcohol or drugs.
(d) Navigational error.
(e) Disregard for speed limits or other boating regulations.
(f) Failure to use available charts and equipment or to have such equipment on board.
(g) Willful or intentional nature of the violation.
(h) Previous coral reef damage caused by the vessel operator.

Penalties assessed according to this section may be doubled for damage to coral reefs located within the boundaries of John Pennekamp Coral Reef State Park.

(4) Whenever any person or the agent of any person knowingly refuses to comply with or willfully violates any of the provisions of this chapter so that such person causes damage to the lands of the state or products thereof, including removal of those products, such violator is liable for such damage. Whenever two or more persons or their agents cause damage, and if such damage is indivisible, each violator is jointly and severally liable for such damage; however, if such damage is divisible and may be attributed to a particular violator or violators, each violator is liable only for that damage and subject to the fine attributable to his or her violation.

(5) If a person or the person's agent as described in subsection (2) fails to comply with an order of the board to remove or alter a structure on state-owned land, the board may alter or remove the structure and recover the cost of the removal or alteration from such person.

(6) All fines imposed and damages awarded pursuant to this section are a lien upon the real and personal property of the violator or violators, enforceable by the Department of Environmental Protection as are statutory liens under chapter 85.

(7) All moneys collected pursuant to fines imposed or damages awarded pursuant to this section shall be deposited into the Internal Improvement Trust Fund created by s. 253.01 and used for the purposes defined in that section.

68B-42.009 Prohibition on the Taking, Destruction, or Sale of Marine Corals and Sea Fans; Exception; Repeal of Section 370.114, Florida Statutes

(1) Except as provided in subsection (2), no person shall take, attempt to take, or otherwise destroy, or sell, or attempt to sell, any sea fan of the species *Gorgonia flabellum* or of the species *Gorgonia ventalina*, or any hard or stony coral (Order Scleractinia) or any fire coral (Genus *Millepora*). No person shall possess any such fresh, uncleaned, or uncured sea fan, hard or stony coral, or fire coral.

(2) Subsection (1) shall not apply to:

(a) Any sea fan, hard or stony coral, or fire coral legally harvested outside of state waters or federal Exclusive Economic Zone (EEZ) waters adjacent to state waters and entering Florida in interstate or international commerce. The burden shall be upon any person possessing such species to establish the chain of possession from the initial transaction after harvest, by appropriate receipt(s), bill(s) of sale, or bill(s) of lading, and any customs receipts, and to show that such species originated from a point outside the waters of the State of Florida or federal Exclusive Economic Zone (EEZ) adjacent to state waters and entered the state in interstate or international commerce. Failure to maintain such documentation or to promptly produce same at the request of any duly authorized law enforcement officer shall constitute a violation of this rule.

(b) Any sea fan, hard or stony coral, or fire coral harvested and possessed pursuant to permit issued by the Department of Environmental Protection for scientific or educational purposes as authorized in Section 370.10(2), Florida Statutes.

(c) Any sea fan, hard or stony coral, or fire coral harvested and possessed pursuant to the aquacultured live rock provisions of paragraph 68B-42.008(3)(a), F.A.C., or pursuant to a Live Rock Aquaculture Permit issued by the National Marine Fisheries Service under 50 C.F.R. Part 638 and meeting the following requirements:

1. Persons possessing these species in or on the waters of the state shall also possess a state submerged lands lease for live rock aquaculture and a Department of Environmental Protection permit for live rock culture deposition and removal or a federal Live Rock Aquaculture Permit. If the person possessing these species is not the person named in the documents required herein, then the person in such possession shall also possess written permission from the person so named to transport aquacultured live rock pursuant to this exception.
2. The nearest office of the Florida Marine Patrol shall be notified at least 24 hours in advance of any transport in or on state waters of aquacultured live rock pursuant to this exception.
3. Persons possessing these species off the water shall maintain and produce upon the request of any duly authorized law enforcement officer sufficient documentation to establish the chain of possession from harvest on a state submerged land lease for live rock aquaculture or in adjacent Exclusive Economic Zone (EEZ) waters pursuant to a federal Live Rock Aquaculture Permit.
4. Any sea fan, hard or stony coral, or fire coral harvested pursuant to paragraph 68B-42.008(3)(a), F.A.C., shall remain attached to the cultured rock.

(3) It is the intent of this rule to effect the repeal and replacement of Section 370.114, Florida Statutes. The Commission has determined that the repeal of this statute will not adversely affect the marine coral resources of the State of Florida.

Chapter 18-20 Florida Administrative Code – Florida Aquatic Preserves

All sovereignty lands within a preserve shall be managed primarily for the maintenance of essentially natural conditions, the propagation of fish and wildlife, and public recreation, including hunting and fishing where deemed appropriate. Aquatic preserves which are described in Part II of Chapter 258, Florida Statutes, were established for the purpose of being preserved in an essentially natural or existing condition so that their aesthetic, biological and scientific values may endure for the enjoyment of future generations. Preserves were established to preserve, promote, and utilize indigenous life forms and habitats, including but not limited to: sponges, soft coral, hard corals, submerged grasses, mangroves, salt water marshes, fresh water marshes, mud flats, estuarine, aquatic, and marine reptiles, game and non-game fish species, estuarine, aquatic and marine invertebrates, estuarine, aquatic and marine mammals, birds, shellfish and mollusks. So, although the Preserves were not intended to specifically protect *Acropora*, these species are protected through the protection of all hard corals.

John Pennekamp Coral Reef State Park

The park was established in 1960 as the first undersea park in the U.S. extending three miles into the Atlantic Ocean along approximately 25 miles offshore of Key Largo. This area was established to protect and preserve a portion of the only living coral reef in the nearshore continental U.S. Combustible engines are not permitted in or near shore areas of the park where the water is less than four feet deep. In general the rules, and protections the Florida Keys National Marine Sanctuary affords corals also apply in this park.

State of Florida Regulatory Programs

Florida has a comprehensive state regulatory program that regulates most land, including upland, wetland, and surface water, alterations throughout the State. The comprehensive nature of the State program is broader than the federal program in that it also regulates alterations of uplands that may affect surface water flows. This regulatory program also includes a Federal-State Programmatic General Permit and implementation of a statewide National Pollutant Discharge Elimination System (NPDES) program. In addition, activities located on or using State-owned sovereign submerged lands also require applicable proprietary authorizations, including consent agreements, leases, and easements.

Outstanding Florida Waters

Marine waters surrounding the Florida Keys have been declared as “Outstanding Florida Waters” (OFW) by the State of Florida (FDEP, 1985). By regulation, input of materials that could be considered pollutants to open surface waters cannot exceed the concentration of those materials that naturally occur in the waters. Because of OFW designation, direct surface water discharges of pollutants have been eliminated or are being phased out in the Florida Keys.

The Florida Keys have also been designated a region of "critical State concern" which requires the development and approval by the Florida Department of Community Affairs a "Monroe County Comprehensive Plan" that addresses elimination of sources of pollution and land-management options.

Environmental Resource Permitting and Wetland Resource Permit

The Environmental Resource Permit (ERP) Program is an independent State permit program that operates in addition to the federal dredge and fill program. The ERP Program regulates activities involving the alteration of surface water flows. This includes new activities in uplands that generate stormwater runoff from upland construction, as well as dredging and filling in wetlands and other surface waters. ERP permit applications are processed by either the Florida Department of Environmental Protection (FDEP) or one of the State's water management districts, in accordance with the division of responsibilities specified in operating agreements. The ERP Program is in effect throughout the State except for the Florida Panhandle (Northwest Florida Water Management District).

In northwest Florida, a Wetland Resource Permit (WRP) (Chapter 62-312 F.A.C.) is required for any dredging, filling or construction in, on, or over waters that are connected (naturally or artificially) to "named waters." Named waters include the Gulf of Mexico, bays, bayous, sounds, estuaries, lagoons, river, streams, and natural lakes that are not wholly owned by one person other than the State. This permitting system does not regulate dredging or filling in isolated wetlands and is implemented solely by the FDEP.

In peninsular Florida, the ERP Program regulates virtually all alterations to the landscape, including all tidal and freshwater wetlands and other surface waters, as well as storm water runoff quality and quantity. This program regulates everything from construction of single family residences in wetlands, convenience stores in uplands, dredging and filling for any purpose in wetlands and other surface waters, construction of roads, and agricultural alterations that impede or divert the flow of surface waters. Application of this permitting program ensures that water quality is not degraded, and that wetlands and other surface waters continue to provide productive habitat for fish and wildlife, including corals.

Issuance of an ERP permit constitutes water quality certification or waiver thereto under Section 401 of the CWA (33 U.S.C. 1341). Finally, issuance of an ERP permit in coastal counties constitutes a finding of consistency under the Florida Coastal Zone Management Program (Section 301 Coastal Zone Management Act).

Submerged Lands Authorization

In addition to the above regulatory program, Submerged Land Authorization is required for any construction on or use of submerged lands owned by the State (sovereign submerged lands) (F.S. Chapter 253). Such lands generally extend waterward from the mean high water line of tidal waters, or the ordinary high water line of freshwaters, out to the State's territorial limit. The State's territorial limit is approximately 3 miles into the Atlantic Ocean and nine miles into the Gulf of Mexico.

If such lands are located within certain designated Aquatic Preserves, the authorization must also meet the requirements of Chapter 258 of Florida Statutes. Such authorization considers issues such as riparian rights, impacts to submerged land resources, and preemption of other uses of the water by the public. Authorizations typically are in the form of consent of use, easements, and leases. This program is implemented jointly by the FDEP and four (of five) of the State's water management districts in accordance with the same operating agreement that governs the ERP Program. The program is structured so that applicants who do not qualify at the time of the permit application for both the regulatory permit and the propriety authorization cannot receive either permit or authorization.

National Pollution Discharge Elimination System

In addition to the State regulatory program, Florida has statewide authorization to implement the Federal NPDES permit program for stormwater. Areas of regulation include municipal separate storm sewer systems, certain industrial activities, and construction activities. New construction may require a stormwater permit if the clearing, grading, or excavation work disturbs five or more acres of land and discharges to either surface waters of the State or to a Municipal Separate Storm Sewer System.

State Programmatic General Permit

In 1997, the Corps delegated to FDEP the authority to issue federal dredge and fill permits under Section 404 CWA for certain activities that qualify for an ERP or WRP permit or exemption. This program is known as the State Programmatic General Permit (SPGP). The SPGP is excluded from Monroe County (Florida Keys) and counties within the jurisdiction of the Northwest Florida Water Management District. The purpose of the SPGP is to avoid duplication of permitting between the Corps and FDEP for minor work located in waters of the U.S. thus eliminating the need for separate approval from the Corps for certain activities. Activities covered by SPGP include:

1. Construction of shoreline stabilization activities (riprap and seawalls); groins, jetties, beach nourishment/re-nourishment are excluded.
2. Boat ramps and boat launch areas and structures associated with such ramps and launch areas;
3. Docks, piers, marinas, and associated facilities;
4. Maintenance dredging of canals and channels;
5. Selected regulatory exemptions; and
6. Selected ERP noticed general permits.

State of Florida Clean Vessel Act and Designation of Waters of the State Surrounding the Florida Keys as a No Discharge Zone

The State of Florida's Clean Vessel Act of 1994 requires houseboats to store sewage in holding tanks (Type III Marine Sanitation Device (MSD)) that must be pumped out and disposed at approved facilities. However, vessels other than houseboats could legally discharge wastewater from Type I or Type II MSD that disinfect the wastewater but do not remove nutrients. For that reason, on July 26, 2001, the USEPA, under authority of

Section 312 of the CWA, published a proposed rule to establish a No Discharge Zone (NDZ) in State of Florida waters within the boundaries of the FKNMS. That action was taken at the request of the Governor of Florida, with support by the Monroe County Board of County Commissioners and the FKNMS Water Quality Steering Committee. The rule became effective in June 2002 and makes it illegal to dump sewage, whether treated or not, into State waters. NOAA is pursuing establishment of a NDZ in federal waters of the FKNMS. The Clean Vessel Act administers a grant program to fund construction of vessel sewage pump out facilities and toilet dump stations at marinas.

Chapter 99-395, Laws of Florida
In 1999, the Florida State Legislature approved Chapter 99-395 that was adopted as a Law of Florida. This law prohibits new surface water wastewater discharges, requires existing wastewater facilities discharging to cease surface water disposal by 2006, and requires all other discharges to meet specific treatment and disposal standards by July 1, 2010. Facilities with flows greater than or equal to 100,000 gallons per day are required to provide basic disinfection and produce advanced waterwater treatment effluent. Facilities with flows less than 100,000 gallons per day and onsite systems (e.g., septic tanks) are required to provide disinfection and produce an effluent that meets best available technology requirements. Facilities with a wastewater flow of 1 million gallons per day or greater must use a deep injection well for disposal, while facilities with flows less than 1 million gallons per day must discharge to a shallow injection well.

Phosphate Detergent Ban in Monroe County, Florida
The Monroe County Board of County Commissioners (Florida Keys) (MCBCC) recognized that phosphate-laden detergents are a significant source of phosphate pollution of canals and other nearshore waters of the Florida Keys. The board also recognized that phosphate enrichment of nearshore waters can result in the growth of nuisance algae and can alter ecosystem structure and function, including coral reefs. The MCBCC passed Monroe County Ordinance 029-1989 in October 1989 making it unlawful for any person, firm, or corporation to sell, offer to expose for sale, give or furnish any detergent containing more than 0% to 0.5% phosphorus by weight within unincorporated and incorporated areas of Monroe County. An exemption is given for detergents used in machine dishwashing that contain 0% to 5.9% phosphorus by weight.

2.2 Puerto Rico

Law for the Protection, Conservation, and Management of Coral Reefs in Puerto Rico, Law 147
In Puerto Rico there exist several laws and proposed regulations that may aid in the conservation of corals, the most pertinent statute of which is the 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. The Department of Natural and Environmental Resources (DNER), the agency in charge of implementing the law, will do so through a regulation that is currently being prepared. Law 147 provides for the creation of zoned areas in

order to mitigate impacts from human activities, including (1) Reef Recuperation Areas and (2) Ecologically Sensitive Areas. These zones will facilitate the DNER in controlling human activity that can directly impact *Acropora* spp. such as anchoring. Law 147 also directs the DNER to identify and mitigate threats to coral reefs from degraded water quality due to pollution, and additionally requires an Environmental Impact Statements (EIS) for projects or activities that can negatively affect coral reefs.

Marine Protected Areas

Law 137 (2000) directs the DNER to designate priority areas as marine reserves, including a minimum of 3% of the insular platform within three years (2003). Marine reserves are defined as areas where all extractive activities are prohibited in order to help recover depleted fishery resources and protect biodiversity; such reserves can protect *Acropora* spp. by preventing impacts from fishery gear. To date, four marine reserves have been established: Luis Peña Channel Reserve in Culebra (1999), Desecheo Island Reserve (2000), Mona Island, Monito Island Reserve (2004), and Tres Palmas Reserve in Rincon (2003). With the exception of Tres Palmas, the marine reserves are all no-take and all have mooring buoys to protect benthic habitats. There are currently an additional 13 natural reserves in Puerto Rico that have coral reefs within their boundaries. These are managed by the DNER and are located on all coasts and offshore islands thus providing an infrastructure for management measures to protect extant *Acropora* spp. populations. The DNER has been utilizing mooring buoys since 1990, principally in the Natural Reserves in Fajardo, Culebra, Guánica, and La Parguera. However more information is needed on the location and status of *Acropora* spp. populations within the natural reserves in order to apply the conservation strategies, particularly those pertaining to direct physical impacts. It should be noted that natural reserves probably have minimal success in preventing impacts to coral reefs and *Acropora* spp. from degraded water quality because reserve boundaries do not prevent these impacts.

Enforcement of marine protected areas in Puerto Rico is patchy due to limited numbers of officers and patrol vessels. As elsewhere, DNER officers are responsible for enforcing a wide variety of marine and terrestrial environmental regulations and are therefore unable to devote sufficient time to patrolling marine protected areas.

2.3 U.S.V.I.

Virgin Islands Coastal Zone Management Act of 1978

According to Virgin Islands Code, T. 12, Ch. 21, Section 906(b)(7), also known as the VI Coastal Zone Management Act of 1978: …"sand, rock, mineral, marine growth and coral (including black coral), shall not be taken from the shorelines without first obtaining a coastal zone permit." This law is generally used to prevent the taking of coral anywhere in the U.S.V.I.

Indigenous and Endangered Species Act of 1990

Virgin Islands Law VIC, T. 12, Ch. 2, Section 103 (a), also known as the Indigenous and Endangered Species Act of 1990: states that "No person may take, catch, possess… any indigenous species, including live rock (includes coral)… without a valid scientific or aquarium collecting permit, or indigenous species retention permit…" Aquarium permits have not been issued except for private aquarists; and no permits for coral collections are approved.

Marine Protected Areas
Virgin Islands law (VIC, T. 12, Ch. 1, Section 97) provides for the establishment of wildlife or marine sanctuaries for the purpose of propagating, feeding and protecting birds, fish and other wildlife (which includes coral). Marine sanctuaries established under this law include:

1. Cas Cay/Mangrove Lagoon Marine Reserve and Wildlife Sanctuary, St. Thomas (1994). This sanctuary includes many acres of mangrove wetlands, shallow seagrass beds and coral reefs. The taking of any living organism or part thereof from this area is prohibited.

2. St. James Marine Reserve and Wildlife Sanctuary, St. Thomas (1994). This sanctuary includes many acres of shallow seagrass beds, coral reefs and some algal plain. The taking of any living organism is prohibited except with a valid scientific collecting permit.

3. Salt River Bay Marine Reserve and Wildlife Sanctuary, St. Croix (1995). This site includes many acres of mangrove wetlands, shallow seagrass beds and coral reefs.

4. St. Croix East End Marine Park (2002). This site includes many acres of shallow back-reef habitats, seagrass beds and fringing and deeper coral reefs. While rules and regulations have not yet been promulgated for this park, the enabling legislation establishes the requirement to zone this area, including no-take zones over much of the inshore area to a line seaward of the fringing/bank reef system. The park will require the use of moorings and other measures to protect benthic habitats.

3 International

Summarized below by nation are conservation actions enacted that include corals or coral reefs. The activity/legislation listed is usually for a specific location within the nation rather than omnipresent.

Bahamas
The Exuma Cays Land-and-Sea Park (1958) is composed of 45,584 ha of small islands and marine areas in the central Bahamas. The park encompasses a 35-km long section of the northern Exuma Cays and was designated a no-fishing zone in 1986, making it the first no-take marine reserve in the wider Caribbean. Subtidal habitats where *Acropora* spp. can colonize include leeward patch reefs, extensive areas of octocoral and sponge-dominated hard-bottom, some smaller fringing reefs, and deeper (12-15 m) spur and

groove reefs (Chiappone and Sullivan 1991, Sullivan and Chiappone 1992). In shallower habitats throughout the Exuma Cays (including areas outside of the park), *A. palmata* is generally rare and is generally restricted to the platforms of islands in water depths less than 5 m (Chiappone et al. 1997a,b). *A. cervicornis* was historically ubiquitous on many fore-reef terraces along the island chain bordering Exuma Sound, but in most places suffered mass mortality from disease by the late 1980s (Chiappone et al. 1997). Coral damage is reported from diving and fishing activities, as well as the use of chlorine bleach for fish collecting. Mooring buoys have been installed at some of the more popular dive sites to minimize anchor damage both inside and outside of the park.

Belize

Hol Chan Marine Park (ca. 1986) is a managed nature reserve located on the south tip of Ambergris Cay, Belize. The park is a 311 ha reef area with associated seagrass beds, and approximately 100 ha of mangrove cays. The site covers a continuum of environments from mangrove cays to lagoon through the Hol Chan Channel, then over the back reef to the reef crest, and then for 1.2km out past the fore reef towards the deep sea. The reef crest and outer reef crest are reported to have abundant *A. palmata*. Fisheries Ordinance Section 9 (A) (1977) and the Wildlife Protection Act (No. 4 1981) relate to this area. Designation has been proposed to prevent overfishing in the area and to help maintain the coral reef ecosystem and enhance tourist attraction.

The Belize Barrier Reef Reserve System is composed of seven marine reserves, national monuments and national parks, all established between 1977 and 1996. They include Bacalar Chico National Park and Marine Reserve (10,700 ha), Blue Hole Natural Monument (4,100ha), Half Moon Caye Natural Monument (3,900 ha), South Water Caye Marine Reserve (29,800 ha), Glover's Reef Marine Reserve (30,800 ha), Laughing Bird Caye National Park (4,300 ha), and Sapodilla Cays Marine Reserve (12,700 ha). The Reserve System is located within the Belize Barrier Reef Complex, which is located only a few hundred meters offshore in northern Ambergris Caye, to about 40 km offshore in the south. The barrier reef presents a zonation pattern which seems to be similar to that described for other reefs in the Caribbean. In the north, the barrier reef touches the shoreline at Rocky Point, maybe one of the few sites in the world where a major barrier reef meets a coast. Outside the barrier reef, there are three large atolls: Turneffe Islands (33,000 ha), Lighthouse (12,600 ha) and Glover's Reef (13,200 ha). These areas are moderately protected under the National Protected Areas System Plan Program for Belize (1995). Funding and staffing constraints have limited protection activities.

British Virgin Islands

The BVI National Parks Trust manages a number of marine sites around the BVI. Most sites are relatively small (10 to 100 ha) and provide protection from anchoring impacts to benthic habitats through the use of moorings.

Cayman Islands

The Cayman Islands Marine Parks are comprised of Marine Park Zones, Environmental Zones, and Replenishment Zones, as well as Designated Grouper Spawning Areas. These zones are scattered around the perimeter of Grand Cayman, Cayman Brac, and

Little Cayman. Marine Park and Environmental zones have prohibitions on the taking of any marine life. Anchoring is prohibited in any hard bottom habitats. Fish pots, nets and spearguns are prohibited in all zones and all corals in Cayman waters are protected by law. These regulations are administered by the Department of the Environment.

Colombia

CORALINA is a public cooperation that was established under Article 37. CORALINA has its own autonomy for administration and its jurisdiction totally encompasses the archipelago of San Andres, Providencia and Santa Catalina in the southwestern part of the Caribbean, off the continental shelf of Nicaragua and Honduras. The mission of CORALINA is to protect and recover natural resources by applying appropriate technologies and furthering community involvement in coastal development. CORALINA used its authorities to establish the Seaflower Biosphere Reserve.

Seaflower Biosphere Reserve (2000) is approximately 300,000 km^2 of marine area and includes offshore islands of the archipelagos of San Bernardo and Rosario and the oceanic archipelago of San Andrés and Providencia. Tayrona National Natural Park, in the central part of the northern coast of Colombia provides limited protection for corals. All three Caribbean *Acropora* species have been listed recently in the "red book" of threatened marine invertebrates of Colombia by a technical commission coordinated by the Ministry of the Environment (Mejía et al., 2002). *Acropora cervicornis* was considered critically endangered species in Colombia, while *A. palmata* was included as endangered, and *A. prolifera* as vulnerable, according to the IUCN categories.

Costa Rica

Gandoca-Manzanillo Ramsar Site (1995) contains approximately 4,436 ha of marine habitats, including well-developed and relatively undisturbed coral reefs. These reefs have higher coral species diversity than other Costa Rican reefs. Management recommendations for this site include a ban on coral extraction and stringent fishing regulations. In addition, Cahuita National Park was established in 1970 to protect one of Costa Rica's only coral reefs on the Caribbean coast; this park includes beaches, mangroves, forests, marsh and 240 ha of adjacent coral reef.

Cuba

Buenavista Biosphere Reserve (2000) in north central Cuba has sea caves and island groups. Its 313,502 ha (58,099 ha core marine area) area is made up of 11 core areas including National Parks, Ecological Reserves, Outstanding Natural Elements, Faunal Refuges, and Protected Areas. Protection for corals varies by protected area status and mandate. The Cienaga de Zapata Biosphere Reserve (2000) in southwestern Cuba is 624,354 ha (28,700 ha core marine area) and contains some of the best-preserved coral reefs in Cuba. The Cuchillas del Toa Biosphere Reserve (1987) in northeastern Cuba is 208,305 ha in area and has a marine core area of 2,642 ha that includes coral reefs, although with high rainfall and many rivers, they are of doubtful significance to *Acropora* spp. The Peninsula de Guanahacabibes Biosphere Reserve (1987) at the west end of Cuba (119,189 ha, 16,400 ha core marine area) contains some of the best-conserved coral reefs in Cuba. All of the biosphere reserves in Cuba have management programs in place to preserve natural resources. Most marine portions of these reserves are located in the core areas, which provides them with the highest level of protection found in a biosphere reserve. However, the degree of protection depends on human resources that is extremely variable across the country.

Dominican Republic

Most of the activities related to non-sustainable fishing practices, as well as industrial, agricultural and rural development, have been either prohibited or regulated by the recently promulgated Environmental Law 64/00 and several Presidential Decrees. Nevertheless the marine ecosystems management is not receiving the sufficient financial and political support needed to support and implement the mandates, policies, enforcement and education. Marine areas under national protection found in the Dominican Republic include Parque Nacional Montecristi, Parque Nacional del Este, and Parque Nacional Jaragua.

Guadeloupe, FWI

The Archipel de la Guadeloupe Biosphere Reserve was created in 1992 and is managed by the National Park of Guadeloupe. The marine portion of the Biosphere Reserve is the Grand Cul-de-sac Marin, 15,000 ha (marine) in size, containing many coral reefs. A management plan was completed in 1998 that directs activities to maintain biodiversity and water quality.

Honduras

The Refugio de Vida Silvestre Punta Izopo is a Ramsar Convention Site (1977). The marine portion of this site contains coral reefs, but no information is available on their status or composition. A management plan was prepared for this Site but appears to be lacking any specific measures for corals.

Cayos Cochinos are a group of two small islands (Cayo Menor and Cayo Grande) and 13 small coral cays lying 19 miles northeast of La Ceiba on the northern Honduran coast. In 1993 a team of business leaders concerned with the conservation of the Honduran coast and its wildlife, together with the Swiss conservation foundation called AVINA, formed the Honduran Coral Reef Foundation (HCRF) that lobbied the Honduran Government to obtain protection for these islands and surrounding waters. In November 1993 Presidential Decree No.1928-93 designated the Cayos Cochinos as a Natural Protected Area and the HCRF as the managing agency responsible for the conservation of the islands. In August 1994 a second Presidential Decree (No. 1704-94) confirmed the protected status of the islands. The protected area covers 460 km^2 and HCRF are responsible for the management of the area. The Cayos Cochinos form part of the second largest barrier reef system in the World known as the Meso-American Barrier reef system and have been identified by the Smithsonian Institution, The Nature Conservancy, World Wildlife Fund, and the World Bank as one of the key sections of the Barrier Reef to preserve. The reefs are the least disturbed ecosystems in the Bay Islands complex and have had a strong and active NGO working with local communities, private sector bodies, and government organizations to help manage the reefs and their fisheries during the last 10 years.

Cayos Cochinos provide a good example of coral reef habitats in the Caribbean and are considered to be less damaged than most Caribbean reefs. However some reefs have been seriously impacted by bleaching, hurricanes, and the impacts of human activity, especially over-fishing. As a result, the local fishing committee has agreed to limit fishing within the protected area to only line fishing and trapping for lobsters within the legal season. Few other protection measures exist.

Jamaica

Pedro Bank and Cays Management Area (1907/1975). The Pedro Bank is roughly triangular in outline, 70 km in its long axis (east-west) and about 43 km in width at the western end. The total shelf area less than 50 m deep is about 8000 km^2, and that less than 20 m deep is about 2400 km^2. The total land area is about 27 ha. The submarine topography is fairly flat, the bottom covered with coral rubble, sand and silt, with patches of scattered corals and algae increasing to the southeast where the cays and reefs and shoals are situated. Little information is available on protection of corals for this area.

Mexico (Atlantic)

Sian Ka'an Biosphere Reserve Coral Reef System, Yucatan Peninsula (1986). Marine portions (120,000 ha) of this reserve contain a wide variety of reef types. Sixteen management zones are identified for this area, with objectives including protection, resource management, monitoring and restoration. The Banco Chincorro Biosphere Reserve (1996) includes 144,360 ha of atoll and platform reef formations. As part of the Mesoamerican Reef System, it is located off the coast of Quintana Roo, eastern Mexico and is reported to contain significant reefs with considerable amounts of *Acropora*. The remote location of this area has provided some protection, however, management objectives are more oriented towards determining the state of the reefs than protection measures at this time.

Netherlands Antilles

Klein Bonaire Island is a Ramsar Convention Site (1980) of less than 100 ha (marine). The island is ringed by fringing reef containing both *A. palmata* and *A. cervicornis* zones. No anchoring or take of corals is permitted. The greatest threat to this site are the approximate 100,000 divers that visit each year. On Bonaire, a marine park was established in 1979, effectively protecting the reef to a depth of 60 m, including Klein Bonaire.

Nicaragua

Cayos Miskitos y Franja Costera Immediata is a Ramsar Convention Site (2001). It contains the Cayos Miskitos Reserve, which is comprised of many small cays, and extensive seagrass intermingled with coral reefs. The site has been designated a Marine Biological Reserve and Protected Area in the Presidential Decree 43-91. The management plan prohibits the take of any species listed as vulnerable or endangered under CITES. All Acroporidae are listed under CITES Appendix II.

Panama

Marine protected areas along the Caribbean coast of Panama include: Isla Bastimentos National Marine Park (132 km^2, established 1988) in the region of Bocas del Toro, Isla Galeta Protected Area just east of the city of Colon, and Portobelo National Park (359 km^2 , established 1976) that includes Portobelo Bay and 70 km of shoreline and coastal waters) east of Isla Galeta (Spalding 2004). These areas have some degree of legal protection, but there has been little active management. The most extensive reefs occur in the San Blas Archipelago, which is controlled by the Kuna people. The presence of the Kuna has protected the San Blas region from extensive development, sedimentation, and pollution, but there has been extensive mining of live corals to enlarge islands (Guzman et al. 2003).

Saba, Netherlands Antilles

Saba Marine Park was established in 1987 and surrounds the entire coast of the island from the high water mark down to the 61 m (200 ft) isobath. The island is an inactive volcano, which rises steeply from the sea. There is a near shore submarine plateau to which coral is restricted, giving way to deep water. The 61 m (200 ft) isobath is never more than 900 m from the shore and is as close as 250 m to the west and east coasts. Along the eastern part of the south coast a shallow, well-developed *A.palmata* zone is present. The aim of the marine park is to ensure conservation of marine resources whilst developing the tourist industry that the coast can sustain. Throughout the park there are regulations, which prohibit the removal of coral and anchoring in coral. The provision of mooring buoys and the designation of an anchorage zone aims to avoid damage, while legislation prohibiting gathering of coral provides a basis for protecting it from collection.

St. Lucia, West Indies

The Soufriere Marine Management Area (SMMA) was established in 1994 and is comprised of a number of zones along the west coast of St. Lucia, many containing considerable amounts of coral reef. Approximately one-third of the entire area is zoned as Marine Reserve, where no fishing or other take is allowed. Anchoring is restricted to sand bottom and it is illegal to take, purchase, sell or possess corals in St. Lucia. The SMMA has been quite successful, as it was established with community input and support and is funded adequately enough to provide a relatively high level of monitoring and enforcement.

Turks and Caicos

The Turks and Caicos Islands (TCI) contain a number of marine protected areas. Some include both marine and terrestrial resources. Marine protected areas are classified as National Parks, Nature Reserves or Historical Sites and all prohibit the take of any marine animal or plant. Of the 19 protected areas that could benefit acroporid corals, ten are entirely marine and nine have both marine and terrestrial components. Strictly marine protected areas range in size from the one-acre Molasses Reef Wreck Area to the 6,532 acre Princess Alexandra Land and Sea National Park. Marine/terrestrial protected areas range in size from the 33 acre Three Marys Cays Sanctuary to the 210 square mile North, Middle and East Caicos Reserve (Ramsar Site).

Effectiveness of the different reserves in TCI depends upon the particular reserve; for example, Princess Alexandra National Park is very well enforced since it is in the area where most of the all-inclusive hotels are located. However, there is a general lack of park officers and rangers and effective patrol boats, yielding a general lack of enforcement and causing many of the protected areas to be essentially paper parks/reserves. Although human impacts to corals are relatively low in TCI (e.g. little sediment runoff or eutrophication), it is felt by managers that they provide little actual protection for acroporid corals. Two recent boat groundings that damaged *A. palmata* resulted in large fines suggesting that the TCI does place significant value on their reefs.

Venezuela

Archipielago de Los Roques is a Ramsar Convention Site (1996) located approximately 180 km offshore of Venezuela. It is comprised of 213,220 ha of shallow waters around the atoll and contains many coral reefs. Management plans call for regulation of small-scale fishing and the harvest of certain species is prohibited. Cuare is another Ramsar Convention Site (1988) in Venezuela, including the Golfete de Cuare, a semi-enclosed body of water. The site contains coral reefs and coral keys, but is significantly impacted by runoff and poor oceanic circulation. The site is managed and protected through PROFAUNA, an autonomous service of the Ministry of Environment and Renewable Natural Resources. Information on specific protections for corals is not available.

The Convention on International Trade in Endangered Species

The Convention on International Trade in Endangered Species (CITES) is a treaty that pertains only to international trade. Species are proposed and accepted by the Conference of Parties to be included in one of several Appendix listings. Species in Appendix I are considered to be in great danger of extinction and all commercial international trade is banned. Species in Appendix II are not considered in danger of extinction, but it is believed that regulation of international trade is necessary to prevent endangerment. Hence, permits are required from the exporting country designating that the export is not detrimental to the persistence of that species in the wild. Such regulation allows for the collection of data on international trade that is often useful in evaluating degree of threat and such data are generally not otherwise available. All scleractinian corals, including *Acropora* spp., are included in Appendix II and, hence, require permitting from the exporting country's Management Authority to transit across international boundaries. CITES Appendix III contains species that are protected in at least one country, which has asked other CITES Parties for assistance in controlling the trade.

The United Nations Environment Programme

The United Nations Environment Programme (UNEP) was established in 1972 to address environmental issues within the United Nations system. UNEP’s mission is to provide leadership and encourage partnering in caring for the environment by inspiring, informing, and enabling nations and peoples to improve their quality of life without compromising that of future generations. UNEP acts as a catalyst, advocate, educator, and facilitator to promote the wise use and sustainable development of the global environment. To accomplish this goal, UNEP works with a wide range of partners, including United Nations entities, international organizations, national governments, non-governmental organizations, the private sector, and civil society. UNEP's work encompasses:

1. Assessing global, regional and national environmental conditions and trends,
2. Developing international and national environmental instruments,
3. Strengthening institutions for the wise management of the environment,
4. Facilitating the transfer of knowledge and technology for sustainable development, and
5. Encouraging new partnerships and mind-sets within civil society and the private sector.

Human-induced environmental change has accelerated over the last three decades, and those changes have been documented in UNEP's Global Environment Outlook reports. Recognizing the need for independent, objective scientific assessment of the causes of environmental changes, UNEP has initiated a process to strengthen the scientific base of UNEP, referred to as the Science Initiative.

Cartagena Convention

The Convention for the Protection and Development of the Marine Environment in the Wider Caribbean Region (Cartagena Convention) was adopted in Cartagena, Colombia on March 24, 1983, and entered in force on October 11, 1986, for the legal implementation of the Action Plan for the Caribbean Environment Programme (UNEP Caribbean Regional Co-ordinating Unit). The Convention has been ratified by 21 United Nations Member States in the Wider Caribbean Region, including the United States. The area of application comprises the marine environment of the Gulf of Mexico, the Caribbean Sea, and areas of the Atlantic Ocean adjacent thereto, south of 30º North latitude and within 200 miles of the Atlantic coasts of the States. The Convention covers various aspects of marine pollution for which the Contracting Parties must adopt measures aimed at preventing, reducing, and controlling:

1. Pollution from ships;
2. Pollution from dumping;
3. Pollution from sea-bed activities;
4. Airborne pollution; and
5. Pollution from land-based sources and activities.

In addition, the parties are required to take appropriate measures to protect and preserve rare or fragile ecosystems, as well as the habitat of depleted, threatened, or endangered species, and develop technical and other guidelines for the planning and environmental impact assessments of important development projects in order to prevent or reduce harmful impacts on the area of application.

The Cartagena Convention has been supplemented by three Protocols:

1. A Protocol Concerning Co-operation in Combating Oil Spills in the Wider Caribbean Region. This Protocol was adopted in 1983.
2. A Protocol Concerning Pollution from Land-Based Sources and Activities. This Protocol was adopted in 1999 and sixteen Member States signed the Final Act to adopt the Protocol. Four States, including Costa Rica, France, Netherlands, and the United States signed the Protocol itself.
3. A Protocol Concerning Specially Protected Areas and Wildlife (SPAW) in the Wider Caribbean Region. This Protocol was adopted in 1990 and entered into force in 2000.

The SPAW Programme supports activities for the protection and management of sensitive and highly valuable natural marine resources. It is responsible for the regionalization of global conventions and initiatives, such as the Convention on Biological Diversity, The International Coral Reef Initiative (ICRI), and the Global Coral Reef Monitoring Network (GCRMN). The objectives of the SPAW Programme are to:

1. Significantly increase the number of and improve the management of national protected areas and species in the region, including the development of biosphere reserves.
2. Develop a strong capability for the co-ordination of information exchange, training, and technical assistance in support of national biodiversity conservation efforts.
3. Develop specific regional, as well as national management plans for endangered, threatened, or valuable species, such as sea turtles, the West Indian manatee, black coral, and migratory birds.
4. Coordinate the development and implementation of the Regional Programme for Specially Protected Areas and Wildlife in the Wider Caribbean, in keeping with the SPAW Protocol.
5. Coordinate activities with the Secretariat of the Convention on Biological Diversity, as well as other biodiversity-related treaties, such as CITES, Ramsar, Bonn, and Western Hemisphere Conventions.

In recognition of the need for collaborative efforts in preserving and protecting the marine environment, the Secretariat to the Cartagena Convention and its Protocols signed a Memorandum of Cooperation with IOCARIBE of the Intergovernmental Oceanographic Commission (IOC) of UNESCO on February 25, 2002. That agreement highlights areas of shared programmatic interest and cooperation between the organizations, both of whom are prepared to promote cooperation and coordination in the wider Caribbean region on activities related to oceanographic conditions, monitoring of marine pollution and management of data generated from those activities.

International Convention for the Prevention of Pollution from Ships (MARPOL)

The International Convention for the Prevention of Pollution from Ships, was adopted in 1973. This Convention was subsequently modified by the Protocol 1978 that introduced stricter regulations for the survey and certification of ships. Together the Convention and Protocol are to be read as one instrument and is usually referred to as MARPOL 73/78.

MARPOL prevents pollution by governing the design and equipment of ships with an established system of certificates and inspections. It requires states to provide reception facilities for the disposal of oily waste and chemicals. MARPOL covers all the technical aspects of pollution from ships, except the disposal of waste into the sea by dumping; it applies to all ships of all types but does not apply to pollution arising out of the exploration of seabeds.

Regulations covering the various sources of ship-generated pollution are contained in six Annexes of the London Convention and are updated regularly. Annexes I and II are compulsory and govern oil and chemicals; Annexes III – VI govern packaged materials, sewage, garbage, and air pollution and are optional. Under the Convention, "special areas" are provided with a higher level of protection than other areas of the sea. The term "special areas" is defined as "a sea area where for recognized technical reasons in relation to its oceanographical and ecological conditions and to the particular character of its traffic, the adoption of special mandatory methods for the prevention of sea pollution by oil, noxious liquid substances, or garbage, as applicable, is required."

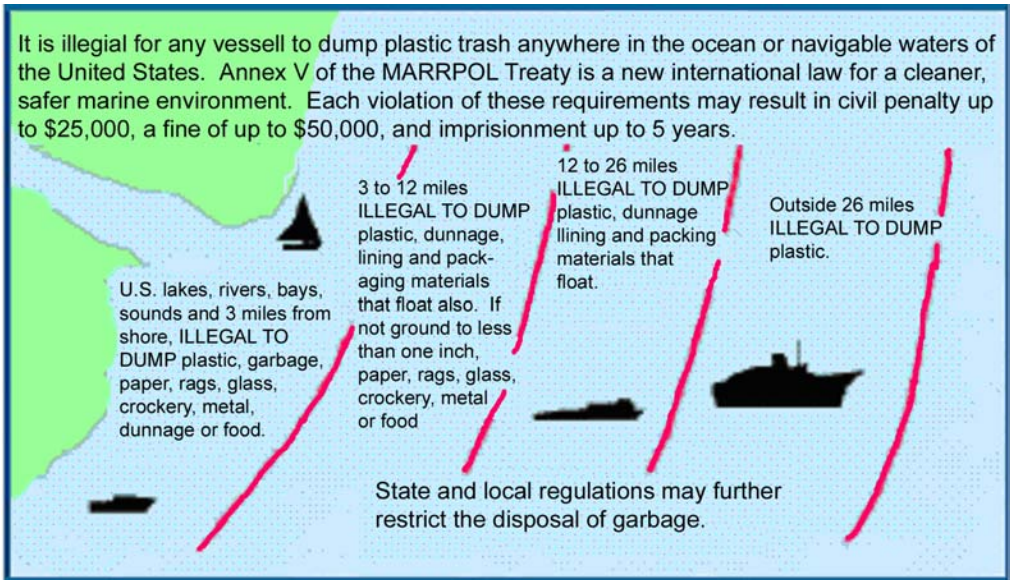
Annex I – Regulations for the Prevention of Oil, entered into force October 2, 1973. This annex details the discharge criteria and requirements for the prevention of pollution by oil and oily substances and it predominantly maintains the oil criteria prescribed in the 1969 amendment to the 1954 Oil Pollution Convention. Besides technical guidelines it contains the concept of "special areas" which are considered to be vulnerable to pollution by oil. Discharges of oil within the "special areas" are completely prohibited, with minor well-defined exceptions.

Annex II – Regulations for the Control of Pollution by Noxious Liquid Substances in Bulk entered into force April 6, 1987. This annex details the discharge and measures for the control of pollution by noxious liquid substances carried in bulk. It subdivides substances and details operational standards and procedures according to substance. Discharge of the residue from these substances is allowed only at the state reception facilities until certain concentrations and conditions are met. In any case, no discharge of residues containing noxious substances is permitted with 12 miles of the nearest land. More stringent restrictions apply to "special areas."

Annex III – Regulations for the Prevention of Pollution by Harmful Substances Carried by Sea in Packaged Form entered into force July 1, 1992. Contains general requirements for the issuing of detailed standards on packing, marking, labeling, documentation, stowage, quantity limitations, exceptions and notifications for preventing pollution by harmful substances. This Annex is implemented through the International Maritime Dangerous Goods (IMDG) Code was entered into force January 1, 1991 and has been amended to include marine pollutants.

Annex IV – Regulations for the Prevention of Pollution by Sewage from Ships entered into force September 27, 2003. This Annex contains requirements to control pollutions of the sea by sewage from ships.

Annex V – Regulations for the Prevention of Pollution by Garbage from Ships entered into force December 31, 1988. This Annex deals with different types of garbage and specifies the distances from land and the manner in which they may be disposed. The requirements are much stricter in a number of "special areas." Notably, this Annex completely bans the dumping of all forms of plastic into the sea and depicted in Figure A-1.



It is illegial for any vessell to dump plastic trash anywhere in the ocean or navigable waters of the United States. Annex V of the MARRPOL Treaty is a new international law for a cleaner, safer marine environment. Each violation of these requirements may result in civil penalty up to $25,000, a fine of up to $50,000, and imprisionment up to 5 years.

U.S. lakes, rivers, bays, sounds and 3 miles from shore, ILLEGAL TO DUMP plastic, garbage, paper, rags, glass, crockery, metal, dunnage or food.

3 to 12 miles ILLEGAL TO DUMP plastic, dunnage, lining and packaging materials that float also. If not ground to less than one inch, paper, rags, glass, crockery, metal or food

12 to 26 miles ILLEGAL TO DUMP plastic, dunnage llining and packing materials that float.

Outside 26 miles ILLEGAL TO DUMP plastic.

State and local regulations may further restrict the disposal of garbage.

Figure A-11. Summary of MARPOL dumping regulations.

Annex VI – Regulations for the Prevention of Air Pollution from Ships and Nitrogenous Emissions (NOx) Technical Code. This annex is awaiting the ratification by 15 states whose combined fleet of merchants constitute at least 50% of the world fleet. This annex contains guidelines and provisions for the emission of different substances and specifies the requirements for the testing, survey and certification of marine diesel engines to ensure they comply with NOx limits. Amendments are being made regularly to the Annex that extend the concept of "special areas," replace lists of substances, design new construction standards, determine reporting requirements and reduce the amount of oil that can be discharged from ships.

The Kyoto Protocol

The Kyoto Protocol calls for industrial nations globally to reduce their emissions of "greenhouse gases" by varying amounts relative to a 1990 baseline, to mitigate climate change, and to promote sustainable development. The protocol is based on scientific research that indicates the Earth is warming because of the accumulation of gases such as carbon dioxide and methane in the atmosphere, chiefly the result of the burning of fossil fuels; these gases are known as "greenhouse gases" because they tend to trap heat on the Eearth. Scientists believe that as the atmosphere warms the weather will become more extreme leading to increases in the number and severity of storms, droughts, and floods.

The Kyoto Protocol puts into place an international system of trading emissions that allows developed countries and companies to gain "carbon credits" for reducing greenhouse gases they produce and for assisting developing countries in plans that reduce emissions. Reducing greenhouse gas emissions can be achieved by improving energy efficiency and switching to renewable sources, such as solar or wind power, or using nuclear power.

With Russia's recent ratification, the Kyoto Protocol came into effect on February 16, 2005. Russia's cooperation (the county accounts for 17 percent of global emissions) allowed the protocol to be ratified by raising the total of participating countries to the required 55%. Both the U.S. and Australia remain outside the treaty, along with developing countries (most notably China) that are not expected to reduce their emissions under the first phase of the treaty, which runs to 2012. When the protocol takes effect, it sets targets for the 30 industrialized nations – excluding the nonparticipating U.S. and Australia – to reduce emissions of six greenhouses gases, most importantly carbon dioxide (a byproduct of coal, oil and gasoline combustion use).

Other UNEP-Sponsored Programs

UNEP has been at the forefront of efforts to protect the world's biological diversity by forging the Convention on Biological Diversity. By administering the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), UNEP helps protect over 30,000 of the world's endangered species. UNEP has also promoted the preparation of the Global Biodiversity Assessment (1995), a major effort to mobilize the global scientific community to analyze the state of knowledge and understanding of biodiversity and the nature of human interactions with it. This work is an independent, peer-reviewed scientific analysis of the current issues, theories, and views regarding the main aspects of biodiversity.

The increasing complexity of environmental degradation requires an enhanced capacity for scientific assessment, monitoring, and early warning. UNEP is implementing or participating in several global environmental assessments, including the Global International Waters Assessment, the Global Environment Monitoring System Freshwater Quality Program, and the Millennium Ecosystem Assessment. Two of UNEP's ongoing programs have a direct impact on the future of coral reef ecosystems, namely the Global Programme of Action for the Protection of the Marine Environment from Land Based Activities (GPA) and the International Coral Reef Action Network (ICRAN).

The goal of the GPA is to prevent the degradation of the marine environment from land-based activities by facilitating the duty of countries to preserve and protect the marine environment. One of the problems the GPA is addressing is the uncontrolled discharge of wastewater into fresh water and coastal environments. Uncontrolled discharges of wastewater are recognized as one of the most serious threats to the productivity and biodiversity of the world's oceans. To address this serious concern, UNEP GPA has worked with The World Health Organization of the United Nations, the United Nations

Human Settlements Programme, and the Water Supply and Sanitation Collaborative Council to develop "Guidelines on Municipal Wastewater Management." The guidelines provide practical guidance on how to plan appropriate and environmentally sound municipal wastewater management systems. The guidelines address the need to link water supply and the provision of household sanitation, wastewater collection, treatment and re-use, cost-recovery, and re-allocation to the natural environment and are summarized in the following ten keys for action:

1. Political commitment;
2. Action at national and local level;
3. Going beyond taps and toilets;
4. Integrated management;
5. Long-term perspectives with step-by-step approaches;
6. Time-bound targets and indicators;
7. Appropriate technology;
8. Demand-driven approaches;
9. Stakeholder involvement;
10. Transparency; and
11. Financial stability and sustainability.

The guidelines target, in part, small island nations that may be surrounded by coral resources and recognize that those biological resources are threatened by destruction and alteration of habitats, changes in hydrology and flow of sediments, overfishing and destructive fishing methods, and the effects of sewage, agriculture, and shipping. The guidelines provide a framework for the development of a "tailor-made" approach to eliminate or reduce the effects wastewater pollution on coastal ecosystems.

In 1992, the United Nations Conference on Environment and Development recognized the importance of coral reef communities and accorded them a high priority for protection. To achieve that goal, the International Coral Reef Initiative (ICRI) was organized in 1994 and consists of governments, non-governmental organizations, academic institutions, and the private sector with the goal of addressing the rapid global decline of coral reefs. ICRI has:

1. Hosted international and regional coral reef workshops to promote global cooperation on sustainable use;
2. Hosted workshops in the United States to foster sustainable use alternatives for local coral communities;
3. Increased awareness of conservation practices among coral nations;
4. Gained cooperative agreements between nations on coral management and conservation;
5. Lobbied the World Bank to consider financing mechanisms for sustainable use of coral ecosystems;
6. Launched the Global Coral Reef Monitoring Network; and
7. Supported the development of marine protected areas, restrictions on fishing methods, and controls on illegal coral trade.

The International Coral Reef Action Network (ICRAN) was established in 2000 and is a global partnership of coral reef experts. The goal of ICRAN is to halt and reverse the decline of the health of the world's coral reefs. ICRAN's partners have created a globally integrated action plan (Framework for Action) to manage and protect coral reefs, based upon recommendations from the ICRI.

ICRAN is the first partnership to respond to conservation needs at the global scale by recognizing both traditional and scientific perspectives of coral reef dynamics and respective social dependency. It seeks to put financial mechanisms in place that support the translation of findings into direct on-the-ground action throughout the world's major coral reef regions.