Title

The threatened Atlantic elkhorn coral, Acropora palmata : population dynamics and their policy implications

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The threatened Atlantic elkhorn coral, *Acropora palmata*: population dynamics and their policy implications

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in

Marine Biology

by

Tali Vardi

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2011

The dissertation of Tali Vardi is approved, and it is acceptable

in the quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2011

DEDICATION

For my dad, Dr. Yehuda Vardi, who infected me with a love for solving puzzles and quizzed me on multiplication tables while tucking me in. I miss you. A lot. Those multiplication skills and a few other things you taught me, such as laughing constantly and making friends with everyone, have come in super handy.

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Finally, for those without a voice, the creatures.

EPIGRAPH

An investment in knowledge pays the best interest.
-Benjamin Franklin

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Chapter 3 is currently being prepared for publication. Vardi, Tali; Hester, Jeff; Sandin, Stuart. The dissertation author was the primary investigator and principal author of this manuscript.

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T Vardi, DE Williams, and N Knowlton. 2010. The ESA at ESA: What population models can offer endangered corals in the face of climate change. Ecological Society of America, 95th Annual Meeting.

T Vardi, DE Williams, and KL Kramer. 2008. What is the future of the Threatened *Acropora palmata*? Population projections and management recommendations. 11th International Coral Reef Symposium.

T Vardi and JP Kritzer. 2007. Metapopulation dynamics and large-scale restoration planning, Alewives on the south shore of Long Island. 65th Annual Northeast Fish and Wildlife Conference.

T Vardi. 2008. *Acropora palmata* population viability analysis. *Acropora* Recovery Team Meeting. (Invited speaker)

ABSTRACT OF THE DISSERTATION

The threatened Atlantic elkhorn coral, *Acropora palmata*: population dynamics and their policy implications.

by

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Professor Stuart Sandin, Chair

Fossil data from multiple locations indicates that Atlantic elkhorn coral, *Acropora palmata*, formed shallow reefs throughout the Caribbean Sea since the Pleistocene. Beginning in the 1980s *A. palmata* has declined to a small fraction of its formerly vast extent throughout the region. In 2006, elkhorn coral was the first coral, along with its sister species, staghorn coral (*Acropora cervicornis*), to be included on the U.S. Endangered Species List. We used size-based matrix modeling to parameterize annual *A. palmata* population dynamics in Florida, over the course of one severe hurricane year (2005) and six calm years (2004, and 2006-2010), incorporating environmental stochasticity as inter-annual variability. We predicted that benthic cover would remain at current levels (4%) for the foreseeable future (until 2030) and beyond (until 2100), suggesting a lack of resilience following the 2005 hurricanes. Standard metrics for the quantification of number and size of individuals are essential to endangered species management. These usually straightforward tasks can be challenging for clonal, colonial organisms. *Acropora palmata* presents a particular challenge due to its plastic morphology and frequent fission. We quantified three-dimensional colony surface area (CSA), the most ecologically relevant measure of size, for 14 prototypically arborescent *A. palmata* colonies using three-dimensional digital imaging software. To relate CSA to simple field metrics, we compared log-likelihood values and determined that planar projection was the best predictor. The, tight, linear relationship between planar projection and CSA enables ecological rates, such as reef accretion and gamete production, to be calculated from field data. Finally, we expanded the matrix population model to compare population dynamics in several locations across the Caribbean. The general trend for *Acropora palmata* is further reductions in population size by 2030. The most striking difference we quantified was between Jamaica, where population size is projected to increase, and all other locations, where population size is projected to remain stable or decline. Density of a key herbivore, the sea urchin *Diadema antillarum*, was an order of magnitude greater in Jamaica than in any other location. These increases are occurring 30 years after a devastating die-off suggesting that herbivory by urchins may facilitate *A. palmata* recovery.

CHAPTER 1: Introduction

OVERVIEW OF THE DISSERTATION

This dissertation includes three empirical data chapters. Each of the chapters is intended to stand alone as a publishable unit, and as a result there is some redundancy in the introductory sections and description of research methods. Below I outline the research objectives of each of the data chapters.

Chapter 2: Short-term population predictions of threatened elkhorn coral in the northern Florida Keys using stochastic matrix modeling

Motivation:

Caribbean acroporids, elkhorn and staghorn coral, are the first marine clonal invertebrates to be included on the U.S. Endangered Species List and are listed as critically endangered on the IUCN Red List. A plan for species recovery is a legal mandate, but the science of coral population and extinction dynamics is not well developed. Although we are less familiar with the population dynamics of clonal as opposed to aclonal organisms, previous studies suggest that non-contiguous colonies vary in vital rates according to their size rather than age (Hughes 1984, Hughes and Connell 1987). Size-structured matrix population modeling informs our understanding of the relative importance of these different size classes, or life history stages, on population expansion and enables a prediction of population size structure to assist with recovery planning.

Clonal organisms evolved to inhabit relatively stable environments (Coates and Jackson 1985). However, elkhorn coral (*Acropora palmata*) inhabits the least stable of reef environments, the reef flat and upper reef crest, where wave energy is high and storms frequently inflict severe damage. This is also the zone of highest resource (food, light) availability and greatest predation intensity; thus, *A. palmata* experiences life in the "fast lane" of coral reefs, where resources are plentiful and growth is fast, but also where punctuated disturbance occurs relatively frequently (Jackson 1991). Population dynamics thus vary to some degree interannually, and markedly during years with severe storms or hurricanes. *A. palmata* matrix population modeling requires parameterization during both storm years and calm years. The Florida Keys, where storms occur frequently, present an ideal study site to parameterize such a model. In 2004, the National Oceanic and Atmospheric Administration Southeast Fisheries Science Center (SEFSC) initiated a seven-year *A. palmata* demographic study. Three hundred individual colonies were identified, tagged, and measured annually. This rich data set allowed a temporally stochastic exploration of *Acropora palmata* population dynamics, the first of its kind for a coral.

Objectives:

2.1 To study the potential importance of large versus small size classes in population persistence using size-structured, temporally (environmentally) stochastic matrix population modeling.

2.2 To predict population density and percent cover of *A. palmata* on the benthos in the near future.

2.3 To estimate (a) the density and (b) the size of outplanting that would be necessary for *A. palmata* to achieve target levels of benthic cover by 2030.

Chapter 3: Quantifying surface area of a structurally complex, endangered reef-building coral, *Acropora palmata*

Motivation:

Three-dimensional colony surface area (CSA) is the mostly ecologically relevant size measurement for any coral, as it relates directly to reef accretion and is proportional to both sexual and asexual reproductive output (Soong and Lang 1992), as well as probability of survival (Hughes 1984, Hughes and Tanner 2000). Because *Acropora palmata* has a complex branching architecture and plastic morphology, surface area cannot be approximated by a simple shape. As such, *A. palmata* surface area has been approximated by various field metrics, but the relationship between those metrics and actual surface area has never been determined. Three-dimensional digital software was used to create digital representations of 14 *A. palmata* colonies from which colony surface area was calculated. Using maximum likelihood, linear models relating this colony surface area to simple field metrics (length, width, and height) and planar projection were parameterized and compared.

Objectives:

3.1 To test the assumption that field metrics adequately describe *Acropora palmata* colony surface area (CSA) as estimated by image analysis software.

3.2 To test whether planar projection (PP, or two-dimensional surface area from a bird's eye view) correlated more tightly with CSA than linear metrics.

3.3 To explore which field metrics (or combinations thereof) correlate most closely with CSA.

Chapter 4: Regional analysis of *Acropora palmata* population dynamics

Motivation:

Anecdotal accounts of remnant *Acropora palmata* populations suggest that current abundances and rates of population depletion or expansion are not consistent throughout the region (*Acropora* Biological Review Team 2005). We learned from Chapter 2 that *A. palmata* populations are indeed dynamic over a less than decadal time scale, and that on extrapolating its current course, Florida's *A. palmata* population is destined for functional extinction. To contextualize this result and to broaden our understanding of this critical ecosystem-building, endangered species, we conducted demographic surveys annually over a minimum of four years in Curaçao (formerly of the Netherlands Antilles) and along the north coast of Jamaica. Curaçao, where hurricanes occur relatively rarely (Bries et al. 2004), was chosen as a contrast to Florida, where hurricanes occur frequently and are a regular source of acute physical destruction and mortality. Disease, bleaching, nutrient concentrations in the water column, and the abundance of herbivorous fish are, of course, also important factors affecting population dynamics. However, the goal here was to determine if trends in population dynamics associated with hurricanes could be distinguished between the two locations. In Curaçao, we expected rates of population growth to be stable (λ approximately equal to 1) and for the stable size distribution to comprise primarily large individuals, as the infrequency of hurricane should lead to relatively undisturbed colony growth (assuming ideal background conditions) and relatively little increase in population size due to colony fragmentation. Jamaica was chosen to represent a population in the process of recovery based on the return of a key herbivore, the sea urchin *Diadema antillarum*, and anecdotal reports on the emergence of young *A. palmata* colonies. In this location, we anticipated rate of population expansion to exceed rates in Florida and Curaçao. Analyses of population dynamics were contextualized with information from three additional locations: Navassa, Puerto Rico, and Virgin Gorda in the British Virgin Islands. In these supplementary locations, demographic data were collected using analogous methods, but only two time points were collected in each location.

Objectives:

4.1 To determine if *A. palmata* dynamics differ significantly across space, as anecdotal evidence suggests.

4.2 To determine the spatial scale of any differences in dynamics, and if any pattern can be discerned.

4.3 To determine if rates of population expansion or depletion (λ) correlate with hurricane frequency or urchin density.

REFERENCES

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

Bries J. M., A. O. Debrot, and D. L. Meyer. 2004. Damage to the leeward reefs of Curaçao and Bonaire, Netherlands Antilles from a rare storm event: Hurricane Lenny, November 1999. Coral Reefs 23:297–307.

Hughes T.P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. American Naturalist 123:778–795.

Hughes T.P., and J.H. Connell. 1987. Population dynamics based on size or age? A reef-coral analysis. American Naturalist 129:818–829.

Hughes T.P, and J. Tanner. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81:2250–2263.

Coates, A., and J.B.C. Jackson. 1985. Morphological themes in marine invertebrates *in* J.B.C. Jackson, L. Buss, and R. Cook (Eds.). Population biology and evolution of clonal organisms. Yale University Press, New Haven. 530pp.

Soong, K., and J. Lang. 1992. Reproductive integration in reef corals. Biological Bulletin 183:418–431.

CHAPTER 2: Short-term population predictions of threatened elkhorn coral in the northern Florida Keys using stochastic matrix modeling

ABSTRACT

Caribbean elkhorn coral, *Acropora palmata* (Lamarck, 1816), was once so widespread and abundant that geologists use its fossils to measure sea level from the Pleistocene through the Holocene. Now it exists at a small fraction of its former abundance and is listed as threatened, along with its sister species, *Acropora cervicornis*, under the U.S. Endangered Species Act. We conducted annual demographic surveys on the northern Florida Keys population from 2004-2010. Percent cover of the benthos, numbers of colonies, and dominance by large individuals declined throughout the study period. We created population matrix models for each annual interval of the study, which included a severe hurricane year (2005-2006). Hurricane recurrence was simulated stochastically along with multiple outplanting scenarios. Further population depletion is predicted given a return time for severe hurricanes of 20 years or fewer. The largest individuals were shown to have the greatest contribution to rate of change in population size via elasticity analysis. Active management through outplanting can provide a positive population trajectory over the short term, especially if larger colonies are transplanted onto the reef. However, the former abundance of this species suggests that life history traits, specifically rates of growth versus shrinkage measured herein, are different from what they must have been in the past. Ultimately, recovery of this species will depend on enacting local short-term management solutions while improving regional and global environmental conditions.

INTRODUCTION

Corals are a recent addition to endangered species lists, and the pace of their inclusion is unprecedented. The Atlantic elkhorn coral, *A. palmata* (Lamarck, 1816), was classified as threatened on the U.S. Endangered Species List along with its congener, *Acropora cervicornis* (Lamarck, 1816), in 2006. Currently, 82 additional corals are considered candidate species (Federal Register 2010). At the international level, the trajectory is similar. In 2008, corals were included on the International Union for Conservation of Nature's Red List for the first time, and 33% of all reef-building corals with sufficient data were listed as threatened (Vulnerable, Endangered, and Critically Endangered), a percentage that surpasses that of most terrestrial animals (IUCN 2011, Carpenter et al. 2008).

Like many listed corals, *Acropora palmata* was neither historically rare nor tightly restricted in its geographic range (Goreau 1959, Geister 1977, Adey 1978). Though there are unexplained gaps in the fossil record (Hubbard et al. 2008), *A. palmata*'s persistence, resilience, dominance, and sheer abundance throughout time and space qualified it as the dominant shallow-water reef builder in the Caribbean from the late Pleistocene through at least the early Holocene (Adey et al. 1977, Jackson 1992, Pandolfi and Jackson 2001, Hubbard et al. 2005, Pandolfi and Jackson 2006, Hubbard et al. 2008). During this time *A. palmata* was dominant on 80% of shallow reefs surveyed throughout the Caribbean and Florida, often forming a monoculture along reef crests and upper reef slopes (Jackson 1992). This percentage dropped to 40% by 1983 and to less than 20% by 1990 (Jackson et al. 2001). Although *A. palmata* is still present throughout its range (Lang 2003), ecological data reveal a continuing decline in abundance. As of 2005, most populations were at 2-20% of 1970s baselines (Bruckner and Hourigan 2000, Carpenter et al. 2008).

The Atlantic *Acropora* Status Review lists the following stressors to *A. palmata*: disease, temperature anomalies and bleaching, natural and anthropogenic branch breakage, competition, predation, excessive sedimentation and nutrification, boring sponges, toxic compounds in the water column, loss of genetic diversity, and others (*Acropora* Biological Review Team 2005). Lists, however, are a deceptively simple presentation of environmental stressors, as feedback loops and synergies lurk between the commas (Kline et al. 2006). Further, lists present a snapshot of a dynamic system in which threats can intensify as population abundance declines. For example, storms can cause direct physical damage and inflict longer-term damage by fragmenting large colonies into smaller colonies that have higher rates of mortality (Lirman 2003, Williams et al. 2006). Multiple storms can result in the decrease of asexual recruitment via fragmentation (Williams et al. 2008). Also, density of corallivorous snails, particularly *Coralliophila abbreviata*, on Atlantic acroporids can increase dramatically after hurricanes, impeding or preventing population recovery (Knowlton et al. 1990, Baums et al. 2003, del Mónaco et al. 2011).

Matrix population modeling can offer a glimpse of the immediate future of a population of *Acropora palmata* colonies. Matrix models use demographic data collected over a time frame appropriate to an organism’s life history, often annual

(Caswell 2001). Data are converted into a matrix of transition probabilities, delineating the likelihood of growing from one life stage to another. Each year the number of individuals in each size class is multiplied by the transition matrix, resulting in a projection of the population size structure for the following year. Hughes (1984) developed a size-based matrix model (an adaptation of the classic age-based matrix model) for organisms with a clonal life history, where size is more important than age and where individuals can not only grow and die but also shrink and fragment (Figure 2-1).

Disturbance is a governing force in coral population structure, and during disturbance events transition probabilities are characteristically different from those during background conditions (Hughes 1984, Fong and Glynn 1998, Edmunds 2010). In the Caribbean, storms and hurricanes are the major physical disturbance events on coral reefs (Gardner et al. 2005) and are thus a critical component for any coral population model. Though *Acropora palmata* is dependent on some level of wave action for asexual reproduction (Highsmith et al. 1980) and sloughing off sediment (Rogers 1983, Acevedo et al. 1989), populations exhibit higher rates of fragmentation (Lirman 2003) and can suffer extreme damage from severe storms (Woodley 1981, Lirman and Fong 1997).

Building on past coral population models, including Lirman's model for *Acropora palmata* (Lirman 2003), we created a stochastic size-based matrix model with disturbance for the *A. palmata* population of the upper Florida Keys. We collected demographic data for seven consecutive years, from 2004 to 2010, from which we estimated annual transition rates for six annual intervals. With this rich data set we simulated a stochastic environment by multiplying the population size structure each year by a random draw from the six matrices, thereby avoiding certain extinction or certain population expansion (which arises from deterministic matrix modeling). During our study, the population experienced severe hurricane conditions in 2005; thus, one snapshot of these disturbance dynamics was captured. Mild storms occurred in the winter of 2004 and summer of 2008 and were considered background conditions, along with 2006, 2007, and 2009. We used our population model to determine critical life history stages, predict future population abundance, explore management actions, and provide a realistic time frame for recovery planning for this population.

METHODS

Study site, data collection, and sampling regime

A rapid survey conducted throughout the Florida Keys from 1999 to 2001 found *Acropora palmata* primarily in high-relief spur and groove reefs, with the upper Keys (off Key Largo) displaying the highest mean percent cover (*Acropora* Biological Review Team 2005), and this area was selected for study. Fifteen non-overlapping 150 m^2 permanent plots, distributed among five reefs (Molasses, French, Elbow, Key Largo Dry Rocks, and Carysfort), were established in 2004. Each plot was circular with a radius of 7 m. Plots were originally chosen to have a minimum density of at least 12 *A. palmata* colonies. Areas of high *A. palmata* density (thickets) are no longer typical in this area and were purposefully avoided so as to manageably track individuals as defined above. For a more detailed description of plot selection, see Williams et al. (2008).

Unlike most population analyses, no attempt was made to distinguish between genets and ramets, as this cannot be done in the field (Miller et al. 2007). Rather, an "individual" was defined as any continuous live tissue or patches of tissue on the same underlying skeleton (for a complete definition, see Williams et al. 2006). Fragments, though producing clones, were considered reproductive output congruent with the definitions presented by Carpenter et al. (2008) and Highsmith (1982) for all corals. Only ramets attached to the substrate, as opposed to loose fragments, were counted as individuals.

Measuring the size of an *Acropora palmata* colony is not straightforward. Unlike a boulder coral, it does not have a consistent shape, and unlike a tree, which bears a morphological likeness to the prototypical *A. palmata* colony, there is no standard measurement such as diameter at breast height (see Figure 2-2). Because corals experience partial mortality, an estimate of the percentage of live tissue is incorporated into our metric. We multiplied the longest axis of the colony (length) and longest perpendicular axis (width) as viewed from above, by a visual estimate of the percentage of live tissue, to estimate two-dimensional projected live surface area, or colony size.

Each year, every colony, including any newly attached individuals (sexual and asexual), was identified and measured (as described in Williams et al. 2006). Surveys were conducted in fall 2004 and each spring from 2005 to 2010. The fall survey was between September 19 and October 22, and spring surveys were between May 1 and July 1. All surveys were completed within an average of four consecutive weeks. In spring 2005, only six of the 15 plots were surveyed, and the remainder were surveyed in the summer. Only those plots surveyed in the spring were used for modeling, but both spring and summer data were used for density estimates.

Designation of size classes

We used size, rather than age or stage, to classify individuals, because size classifications lend themselves more easily to estimates of percent benthic cover of *Acropora palmata* on the reef, which is ultimately our topic of interest. Further, Hughes and Jackson (1985) as well as Hughes and Connell (1987) showed that size has a stronger influence than age on demographic rates, and Lirman (2000) demonstrated this for *A. palmata* specifically. In *A. palmata*, because larger colonies have more branches, and because branches fragment to produce asexual recruits, size is correlated with asexual recruitment. Further, living surface area is positively correlated with the amount of gametes produced (Soong and Lang 1992). We used two-dimensional projected surface area, which is directly proportional to three-dimensional surface area, as our size metric (Holmes and Johnstone 2010, Vardi unpubl.).

Four size classes were defined based on details of the biology and life history of *Acropora palmata*. Size class 1 (SC1) was defined to include all individuals smaller than 100 cm^2, as the highest linear extension rate measured in the Florida Keys is 10 cm/year (in *Acropora* Biological Review Team 2005). Thus a new sexual recruit, unseen in the previous year's survey, could, ostensibly, grow for one year and still be a member of the smallest size class. We chose an upper limit of 900 cm^2 for size class 2 (SC2) because colonies up to this size typically have a low clonal fecundity because they are less likely to have long branches. Size class 3 (SC3) individuals are more likely to have long branches than SC2 individuals, leading to a higher probability of asexual reproduction, but are less than 4000 cm^2, at which size approximately 90% of colonies produce gametes (Soong and Lang 1992). Size class 4 (SC4), those colonies larger than 4000 cm^2, are the most likely to reproduce by both sexual and asexual means.

Model development

Population matrix modeling (Hughes 1984, Caswell 2001) was used to explore *Acropora palmata* demography, using the equation

$n_{t+1} = \mathbf{A} n_{t+1}$,   (1),

where n_t is a vector of the number of individuals in each size class at time t. A square matrix with dimensions equal to the number of size classes, **A**, is the sum of a transition matrix, **T**, and a fertility matrix, **F** (see Figure 2-1).

Each value in **T**, t_{ij}, represents a probability of transitioning from size class j to i from one time point to the subsequent time point. These transition probabilities are estimated by summing the number of times this transition occurs over a particular duration and dividing by the number of individuals in j. Because the abundance per size class changes each year, each transition is based on a different sample size (see Abundance in Table 2-1). Corals can grow (*g*), shrink (*s*), or stay the same size (*l*), thus all positions in **T** can be > 0 (see Figure 2-1a-c). Entries in the fertility matrix, f_{ij}, are based on the number of new individuals that arrive in the study area during the same time interval (see Figure 2-1d). Since sexual recruitment in *A. palmata* is rare (Bak and Engel 1979, Edmunds and Carpenter 2001) and sexual and asexual recruits cannot be distinguished in the field (Miller et al. 2007), we combine these two categories.

We assumed a closed population, where new fragments arise from the existing stand of colonies and can be of any size class (though new SC4 fragments were not observed during this study). New SC3 fragments were assumed to derive solely from pre-existing SC4 colonies (see Figure 2-1d). New SC1 and SC2 fragments were assumed to derive from existing SC3 and SC4 colonies proportionally, based on the ratio of mean size of SC4 colonies to that of SC3 at the beginning of the time step. For $i = 1$ or 2, each year

$$r_i = (f_{i3} \text{ x } n_3) + (f_{i4} \text{ x } n_4) \qquad (2),$$

where r_i is the number of new i-class fragments at the end of the time step, f_{i3} and f_{i4} are the probabilities that an i-class fragment is produced by a SC3 or SC4 colony, and n_3 and n_4 are the number of SC3 and SC4 individuals at the beginning of the time step. Given that q is the ratio of mean size of SC4 to that of SC3 in a given year, we define:

$$f_{i4} = q \text{ x } f_{i3} \qquad (3).$$

Finally, combining (2) and (3) we calculate the fecundity of SC3 as:

$$f_{i3} = r_i \div [n_3 + (q \text{ x } n_4)] \qquad (4).$$

From the seven surveys, six matrix models were developed, one for each time period: 2004-2005, 2005-2006, 2007-2008, 2008-2009, and 2009-2010 (see Figure 2-4). Since the first time period was six months, and all others were annual, the first matrix was squared to make it comparable to the remaining matrices (Caswell 2001). Performing this calculation assumes that transition and recruitment from fall to spring are equivalent to those from spring to fall. However, projections that were run without these data from 2004-2005 showed the same qualitative output.

Model analysis

Long-term rate of change in population abundance, λ, and stable size distribution were calculated by taking the eigenvalue and right eigenvector of each matrix. In addition, stochastic growth rate, λ_s, was estimated from the average growth rate over a long (50,000 year) simulation (Caswell 2001, Stubben and Milligan 2007). Since each matrix captures annual variation in population dynamics (i.e. a stochastic environment), λ_s yields a more robust estimation of the long-term rate of change than any annual matrix or even the mean matrix can provide. In all cases simulations matched Tuljapurkar's approximation for the same parameter (after Stubben and Milligan 2007). Several calculations utilize the mean matrix, $\mathbf{A}_m$, which is simply a matrix with dimension equal to that of **A**, wherein each element a_{ij} is the arithmetic mean of the corresponding a_{ij} from each matrix. Finally, elasticity values,

$$e_{ij} = a_{ij} / \lambda \times \partial \lambda / \partial a_{ij} \qquad (5)$$

were calculated to determine the relative contribution of each of the matrix elements on λ (Caswell 2001). These calculations utilized the "popbio" package in R (Stubben and Milligan 2007).

Population projection and scenarios

From a management perspective, it is critical to explore population projections among likely environmental scenarios. For *Acropora palmata*, one of the most important and variable physical forcings on remnant populations is hurricanes. Physical breakage in the 2005-2006 hurricane season accounted for more tissue loss than any other factor over the course of seven years (Williams and Miller, *in press*).

Bleaching and disease often follow major disturbance events (e.g. Yee et al. 2011) and indeed acute tissue loss due to disease in 2005-2006 was equivalent to background tissue loss throughout the other six years of the study. For brevity, we refer to the disturbance year of 2005-2006 as a “hurricane” year, but the associated detrimental effects from disease are implicit in the quantified transition rates. Frequency of major hurricanes is defined as $1/h$, where h is the return time in years. During 2005-2006, two severe hurricanes (Category 3 or greater) traveled directly through the study area, causing significant damage to the existing population. Single storms can produce a net gain in terms of population abundance, via branch breaks. However, consecutive storms can (and did) result in a net loss, when fragments are swept away before reattachment can occur. Based on annual data collected since 1851, we calculated the return time of two or more severe storms occurring within a 200 nm radius of our study area to be 20 years (NOAA 2011). Thus $h = 20$ represents the most realistic scenario for a stochastic simulation. To bound these results, we explored two alternate return times. As a lower bound, we assumed that our study period was representative, making the implicit assumption that a year as bad as 2005-2006 recurs every six years ($h = 6$). As an upper bound, we assumed a year as bad as 2005-2006 would never return ($h = \infty$). We thus modeled stochastic population projections by randomly selecting one of the six annual matrices, where the probability of selecting the hurricane matrix was $1/h$ and the probability of selecting each of the other five matrices was equal and defined as $[1-(1/h)] / 5$. All hurricane scenarios were run for 20 years (until 2030) and for 50 years (until 2060) in order to contextualize the earlier time frame and to show any potential differences between relatively short- and long-term dynamics.

One of the few *Acropora palmata* management actions available is outplanting colonies reared in nurseries. We simulated outplanting both SC1 and SC2 colonies at three density levels, 1000, 2000, and 3000 outplants over the 2300 m^2 study area, that match density levels currently used for *Acropora cervicornis* (Sean Griffin, personal communication). We did not modify transition rates for outplants but rather assumed that the same rates of growth, shrinkage, and mortality would apply. Mean rates of mortality measured in our study, 30% and 21% for SC1 and SC2 respectively, roughly matched that of similarly sized *A. cervicornis* outplants (20%; Tom Moore, personal communication). The 20-year period is comprised of two years with no planting, five years with planting, and an additional 13 years with no planting. Results are shown after five and 20 years (in the years 2017 and 2030). All outplanting scenarios were projected using h = 20 years. We used size-class specific abundances in 2010 to seed all population projections (see Table 2-1).

Percent cover was calculated by multiplying the number of individuals in each size class in the final year of the projection by the mean size of the corresponding size class (see Table 2-1), and dividing the sum of those numbers by the total study area (2309 m^2). This method assumes that colonies do not overlap, thereby potentially overestimating total percent cover for any projection. All calculations were conducted using R (R Development Core Team 2011). All confidence intervals presented are at the 95% level.

RESULTS

Annual surveys

During the course of our study from 2004 to 2010, *Acropora palmata* cover decreased 40%, from 6.6% to 3.9%, and abundance decreased 21%, from 340 to 269 individuals (Figure 2-3ai,bi). In addition, mean size within each size class declined by 13%, 19%, 1%, and 18% for SC1 through SC4, respectively. The proportion of individuals classified as reproductively viable (including sexual and asexual reproduction, i.e. SC3 and SC4) declined from 52% in 2004 to 42% in 2010 (Figure 2-3ci).

Matrices

Mortality was highest for the smallest size classes and decreased with each successive size class (see Figure 2-4). Probabilities of shrinkage from one size class to the next were as high as 0.22, and rates of growth from one size class to the subsequent were as high as 0.24. Growing two size classes in one year was uncommon (occurring twice) in comparison to shrinking more than one size class, which occurred a total of eight times. The number of new fragments in a given year ranged from 10 to 58, with smaller recruits consistently outnumbering larger ones.

Most commonly, individuals tended to remain in the same size class from one year to the next (Figure 2-4). Over all years and all size classes, the probabilities of stasis (the loop probabilities along the main diagonal of the matrix) were larger than any other probability per size class per year. SC4 had the highest probability of stasis, experiencing zero mortality in all years except 2005-2006. The elasticity of SC4 surviving and not shrinking, e_{44}, was greater than that the elasticity of any other matrix element, e_{ij}, across all years (Figure 2-5), meaning that adult survival had the largest contribution to population growth rate, λ, compared with all other transitions. This was true during background conditions (Figure 2-4a,c-f), as well as during severe storm conditions (Figure 2-4b).

The dynamics of *Acropora palmata* during a severe hurricane year were captured in the 2005-2006 population matrix (Figure 2-4b). Survivorship during this year for all size classes was markedly lower than that for all other years (0.44, 0.53, 0.70, 0.84 for 2005-2006 for SC1-SC4, respectively, versus mean ± SE, 0.76 ± 0.04, 0.84 ± 0.03, 0.95 ± 0.03, 1.00 ± 0.00 for the other five years). Similarly, the probability of growth (Figure 2-1a) for all size classes in 2005-2006 was less than that of background years by one order of magnitude (mean ± SE, 0.01 ± 0.00 versus 0.10 ± 0.01, based on the mean matrix for those years).

Annual population growth rate, λ, calculated from each matrix ranged from 0.71 to 1.05 (Table 2-1) and was 0.96 based on the mean matrix. As such, for every 100 colonies, an average of four died each year. Since 2005-6 was an extreme year, stochastic growth rate, λ_s, depends on the probability of its recurrence, $1/h$, and was estimated for $h = 6$ as 0.956 (95% CI = 0.955-0.957), for $h = 20$ as 0.999 (95% CI = 0.998-1.000), and for $h = \infty$ as 1.019 (95% CI = 1.018-1.020). Thus, assuming a year like 2005-2006 recurs every 20 years, the population of *Acropora palmata* is slowly declining.

Projections

By 2060, without intervention and under a modest hurricane recurrence scenario (h = 20), projected benthic cover of *Acropora palmata* (mean = 4.5%, 95% CI = 0.9-11.2%) is nearly unchanged from that in 2010 (3.9%) (Figure 2-3aiii). Predicted mean abundance in 20 and 50 years is also nearly equivalent to starting abundance (Figure 2-3biii). Note that the estimated stochastic growth rate for h = 20 was estimated as slightly less than 1 (0.999), while short-term projections (20 y and 50 y) suggest slightly positive growth. This distinction is due to the time scales of estimation; λ_s is calculated as the endpoint of a 50,000 y simulation, while these projections were on decadal scales.

Abundance and percent cover change predictably with h. When h = 6, mean cover is reduced to less than 2% by 2030 and less than 1% by 2060 (Figure 2-3aiii). When $h = \infty$, a modest increase in cover to 5.7% (95% CI = 4.3-7.5%) is projected in 20 years, and a doubling of population abundance is projected for 2060. Proportion of individuals in each size class by the end of any projection of 20 years or more (including outplanting projections) is equivalent to the stable size distribution derived from the mean matrix. The convergence to a stable size distribution could occur as early as 8.6 years, using the approach for estimating time to convergence from Doak and Morris (1999).

Finally, size of outplants matters. At the most dense outplanting scenario (1.3 outplants m^{-2} or 3000 outplants over the 2300 m^2 study area), cover using SC2 outplants (mean 47%, 95% CI = 23-61%) is significantly higher than that using SC1 outplants (mean 15%, 95% CI = 7-22%) after five years of outplanting (Figure 2-3bi).

Analogous comparisons of the other SC2 outplanting densities, 0.43 m^{-2} and 0.87 m^{-2} (1000 and 2000 outplants 2300 m^{-2}), reveal a similar pattern resulting in higher percent cover, though confidence intervals are overlapping. Even in the worst-case scenarios (i.e. lower confidence boundaries), five years of SC2 outplantings are predicted to increase percent cover from current conditions (dotted line, Figure 2-3bi). This relationship holds at least until 2030. The same is not true for the SC1 outplanting scenarios. Interestingly, although abundance is predicted to decline between 2017 and 2030 for all outplanting scenarios (Figure 2-3bii), mean percent cover is predicted to increase (Figure 2-3aii). Comparing the proportional size class distribution at 2017, dominated by SC1 and SC2 individuals, to that in 2030, which has a more even size class distribution (Figure 2-3cii), we see that the increase in percent cover is due to growth of outplants into bigger size classes over time.

DISCUSSION

Modeling results

During the seven years of our study, we saw declines in percent cover and mean size of individuals. The demographic rates we measured reveal that, while this population of *Acropora palmata* could persist at or near presently low levels of abundance for the next 50 years, without active management the population will not recover.

Although the population growth rate, λ, is the standard currency of matrix population biology, it can be a misleading metric when applied to the life history of clonal sessile organisms if size structure is not considered. Our most realistic assessment of λ is just below 1.00 (at $h = 20$), not a drastic figure for a threatened species. However, we documented a shift in size structure from the inception of the study, where larger, reproductive size classes with high survivorship dominated (52%), to the end of the study, where smaller, pre-reproductive size classes with lower survivorship dominated (58%). This trend is confirmed by the stable size distribution of the mean matrix, which provides the best estimate of how the size classes ultimately will be distributed. Here, smaller size classes also dominated (56%). Similarly, Hughes and Tanner (2000) saw a shift in dominance from largest to smallest size class in two coral species over a 16-year study period (the third species underwent a significant reduction in average size of the largest size class). These patterns are slow to emerge yet are a critical sign of decline in the overall health of coral populations, as smaller sizes in general have lower survivorship and fecundity (Highsmith 1982, Hughes and Jackson 1985).

Note that confidence intervals widen as the projection interval gets longer, a phenomenon common to all stochastic simulations. Thus the wide confidence intervals on abundance and percent cover estimates can be considered either representative of a stochastic environment or an artifact of our model choice. Prior coral simulation models set the return time of a storm deterministically at varying intervals and simulated background conditions in the interim years (e.g. Hughes 1984, Lirman 2003, Edmunds 2010). There is utility in this approach, as it quantifies the resilience of corals to storms. Further, this is the only option unless more than two demographic surveys have been conducted. We felt our time series was sufficiently long to simulate a stochastic environment and assign a probability of hurricane recurrence. This means that some simulations will have more “bad years” than others, and the resulting response variables thus have a wide confidence interval. Here we present results using a CI of 95%, but from a managerial perspective, focusing on the lower limit of a narrower CI might be more appropriate.

Management recommendations

The top three stressors to *Acropora palmata* in the upper Florida Keys – fragmentation, disease, and snail predation – accounted for 85% of tissue loss over the study period (Williams and Miller, *in press*). All three stressors occur as background conditions, but outbreaks of fragmentation and disease also appear as punctuated sources of mortality in 2005, resulting in significant tissue loss. Snail predation occurred solely as a background source of mortality and had the lowest rank, accounting for approximately 15 m^2 of tissue loss over the seven-year study. Fragmentation due to the hurricanes in 2005 ranked highest, accounting for approximately 30 m^2 of lost tissue over a few months. A disease outbreak during the hurricane months caused an additional loss of 15 m^2, whereas background tissue loss due to disease was 15 m^2 over the seven-year study (Williams and Miller, *in press*). Thus, fragmentation was the largest single factor affecting the *A. palmata* population in our study, followed by disease, then predation.

Fragmentation, due primarily to storms, cannot be stopped (though rescued fragments can be stabilized), and coral diseases are currently incurable. Snails, however, can be removed from colonies. *Coralliophila abbreviata* is a known threat to already depressed acroporid populations, capable of destroying remnant populations in the months and weeks after a storm (Knowlton et al. 1981, Knowlton et al. 1990, Baums et al. 2003). Indeed, incidence of *C. abbreviata* increased fourfold over the course of this study and accounted for 25% of lost live tissue, excluding that from the severe storm in 2005 (Williams and Miller 2010). Interestingly, the proliferation of snails could be a result of overfishing lobsters. Snail removal has been shown to preserve 75% more live *A. palmata* tissue compared with controls where snails are left in place (Miller 2001). Importantly, this management action can target SC4 colonies, which have the greatest influence on population increase, as demonstrated by the elasticity analysis (Figure 2-5).

Outplanting is currently the only recovery strategy being actively pursued by managers. Outplanting can provide a short-term boost to currently depressed demographic rates while long-term strategies to improve environmental conditions are being pursued. We limited these projections to 20 years, as models predict short-term trajectories best, and the influx of colonies leads to a widening of confidence intervals. Unsurprisingly, after five years of planting, abundance is higher and distribution is dominated by whichever size class was planted. Thirteen years after planting, the size class distribution stabilizes, and while mean abundances decrease relative to the 2017 projections, mean percent cover estimations increase relative to 2017. Though many outplants are dying and shrinking, the remainder are growing from SC1 or SC2 to SC3 and SC4, leading to an overall increase in the amount of *Acropora palmata* tissue on the reef during this time period.

We found that planting 3000 SC2 colonies (mean diameter 19 cm) resulted in significantly higher mean percent cover by 2017 than planting 3000 SC1 colonies (mean diameter 6.5 cm) over the study area (1.3 outplants m^{-2}). Furthermore, although planting SC1 colonies could increase cover to 60% by 2030 under the best conditions (upper CI boundary), managers would be wise to focus also on the value of the lower CI boundary, which represents unfavorable conditions; here cover could make a far more modest improvement (9%) over current conditions (4%). In contrast, planting 3000 SC2 colonies results in a worst-case scenario (lower CI boundary) of 24% cover. Thus, according to our model, a dense, five-year SC2 outplanting regime does a fair job of preventing population collapse in terms of both percent cover and abundance.

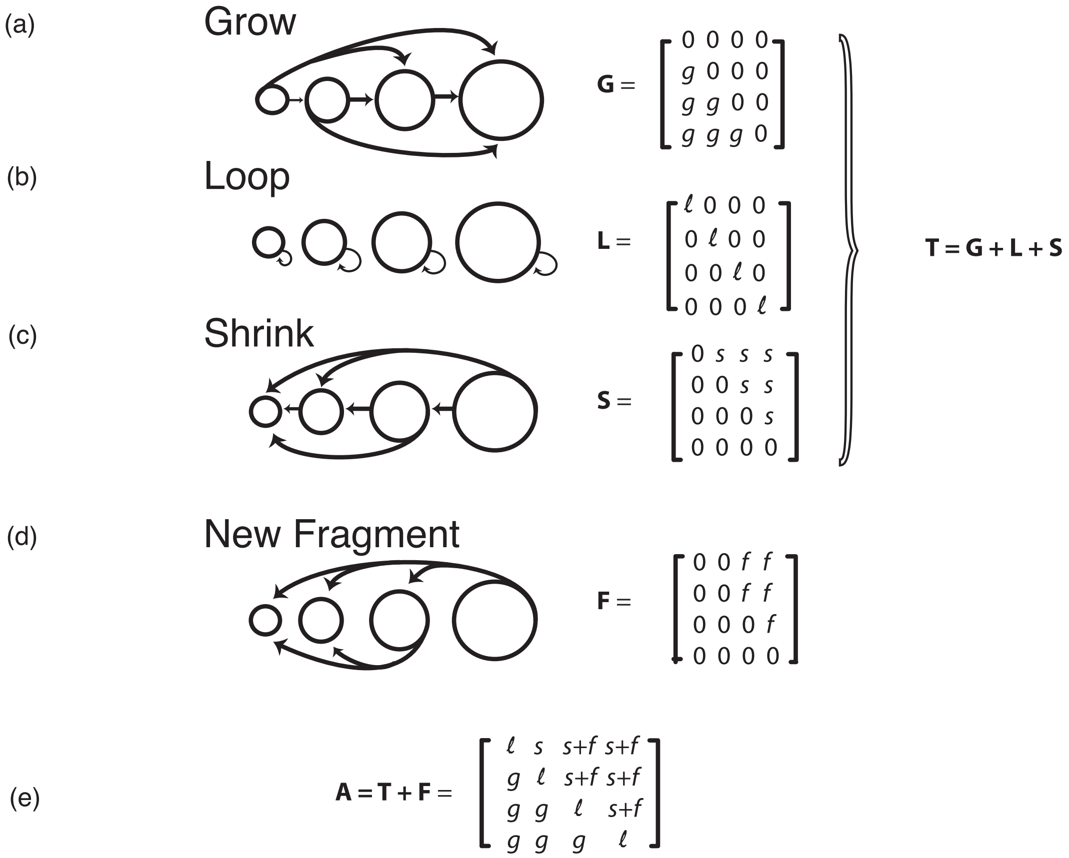
Why does an influx of small individuals only slightly improve population projections? The first explanation is that the smaller size classes do not have a significant influence on population growth (Figure 2-5). The relatively slow growth and high mortality of the individuals limit their demographic potential for the population. But the more relevant question is: Why, even if we eliminate the possibility of a “bad year” ($h = \infty$), does this population seem incapable of recovering? Quite simply, the probability of shrinking, across all size classes and years (mean ± SE, 0.089 ± 0.014), is roughly equivalent to but slightly greater than that of growing (0.082 ± 0.019). This implies that stressors causing the loss of tissue (e.g. disease, predation) are keeping pace with *Acropora palmata*'s ability to thrive, even in the absence of hurricanes.

Our findings are somewhat in contrast to Lirman's (2003) stage-based population model of *Acropora palmata* in the upper Florida Keys, and the difference could highlight an important aspect of this organism’s population dynamics and potential for recovery. Lirman parameterized his model from 1993 to 1997 on Elkhorn Reef, which at the time had a higher density of colonies than the sites described in the present study. In Lirman’s projections, storms recurring every five years resulted in a fourfold increase, from 10 to 50 colonies, after 50 years. (A starting point of 10 colonies was chosen arbitrarily and does not represent density at the site.) In contrast, in the present study, parameterized a decade later with storms occurring every six years (i.e. a slightly more detrimental storm frequency), abundance decreased by 80%, from 270 to 45 colonies (95% CI = 3-186 colonies), after 50 years. The storms and/or the way storms were parameterized could account for this difference; however, relative changes in transition matrix elements for background and storm matrices, especially in the influential rate of stasis for the largest colonies, were comparable in the two studies. Alternatively, *A. palmata* could exhibit positive density dependence, wherein denser stands recover more quickly from storms than less dense stands. This hypothesis should be explored, for example during outplanting, as a density-dependent model could demonstrate that percent cover could increase more quickly than our projections suggest.

Conclusions

Despite being protected under the U.S. Endangered Species Act and being contained within a no-take marine reserve, our results show that without intervention, *Acropora palmata* in the Florida Keys will likely become functionally extinct in the near future. With intervention, population projections are highly variable, but this offers the only positive prospect in the short term. Removing snails would likely have a net positive effect on population trajectories. Outplanting should only be employed in concert with the hard work of improving environmental conditions over the medium term, such as removing excess nutrients from sea water and restoring herbivorous fishes and invertebrates that remove harmful algae, and over the long term, such as reducing sea surface temperature and ocean acidification. Without these measures, new outplants will be doomed to functional extinction just as the current population is.

Eighty-two coral species are currently being considered for inclusion on the U.S. Endangered Species List, none of which has demographic data comparable to that of the *A. palmata* population studied herein. If environmental conditions improve and outplanting provides the predicted buffer against complete elimination, the much-studied and cared for reefs of Florida could provide an excellent example of how to bring a clonal, sessile, endangered organism back from the brink of extinction. We hope that the model presented here will provide context in the potential listing and recovery planning of the candidate species as well.



$$\mathbf{G} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ g & 0 & 0 & 0 \\ g & g & 0 & 0 \\ g & g & g & 0 \end{bmatrix}$$

$$\mathbf{L} = \begin{bmatrix} \ell & 0 & 0 & 0 \\ 0 & \ell & 0 & 0 \\ 0 & 0 & \ell & 0 \\ 0 & 0 & 0 & \ell \end{bmatrix}$$

$$\mathbf{S} = \begin{bmatrix} 0 & s & s & s \\ 0 & 0 & s & s \\ 0 & 0 & 0 & s \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & f & f \\ 0 & 0 & f & f \\ 0 & 0 & 0 & f \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

$$\mathbf{A} = \mathbf{T} + \mathbf{F} = \begin{bmatrix} \ell & s & s+f & s+f \\ g & \ell & s+f & s+f \\ g & g & \ell & s+f \\ g & g & g & \ell \end{bmatrix}$$

Figure 2-1: Life cycle diagram and corresponding matrices. Size classes 1 to 4 are represented by increasing circle sizes. (a-c) Individuals can transition from one size class to any other; they can grow, g, loop (stay in the same size class), l, or shrink, s, comprising the transition matrix, **T**. (d) Arrival of new fragments, represented by the **F** matrix, is defined to include new asexually or sexually derived colonies in any of the three smallest size classes. (e) General form of the matrix model, **A**. Subscripts are left off for clarity. Figure modified with permission from Hughes 1984.

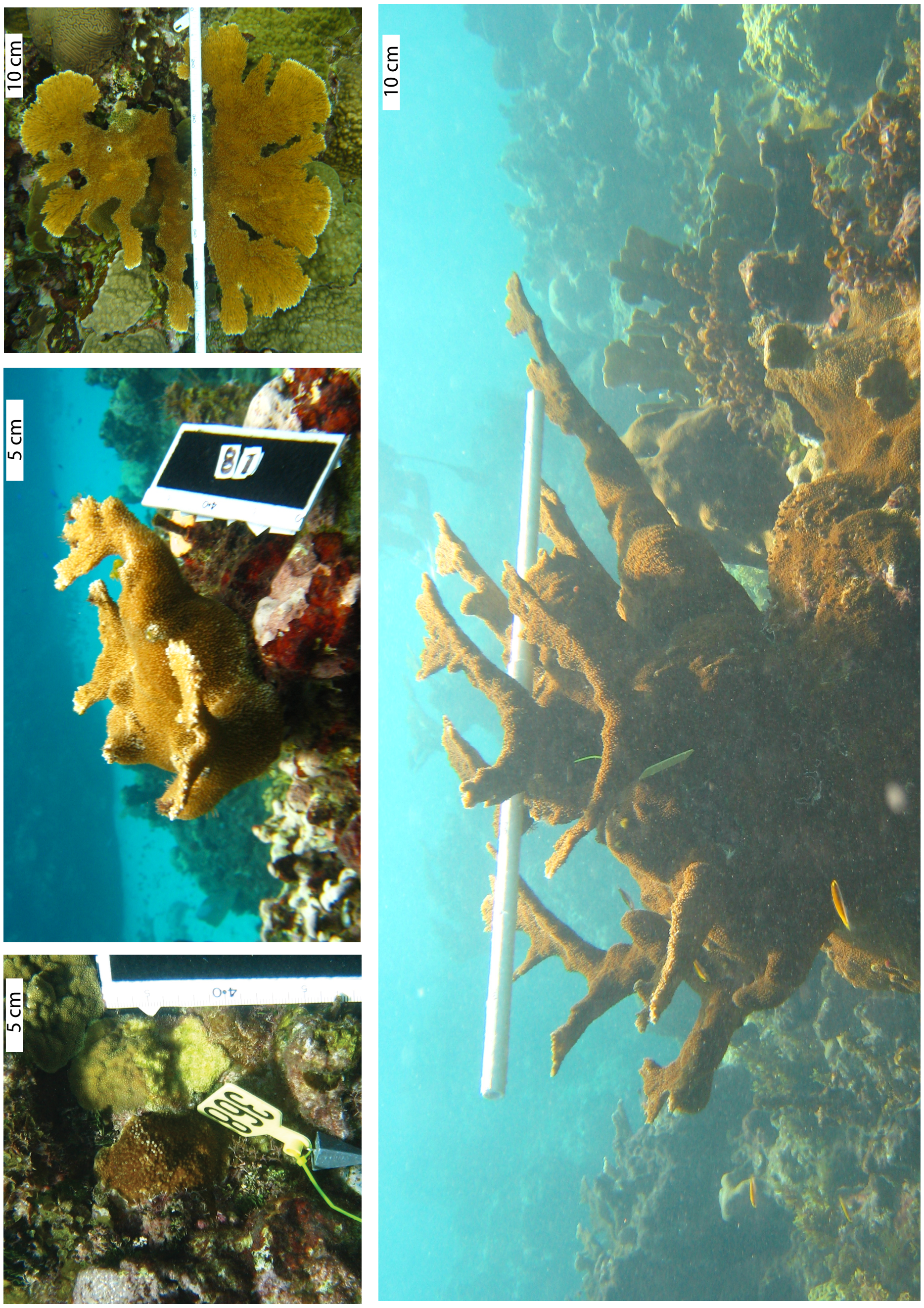


Figure 2-2: Examples of *Acropora palmata* colonies in size classes 1 to 4, clockwise from top left. Size classes are defined as 0-100 cm^2, 100-900 cm^2, 900-4000 cm^2, and > 4000 cm^2, and mean diameters observed were 6.5 cm, 19 cm, 46 cm, and 106 cm for size classes 1 to 4, respectively.

Table 2-1: Summary of size range, mean size, and abundance of individuals per size class, as well as stable size distributions and population growth rate (λ) based on the respective population matrices in Figure 2-4. The superscript ^{a} represents a smaller sample size. In 2005, only six of the 15 plots were surveyed in the spring; therefore, transition and recruitment rates for 2004-2005 and 2005-2006 were calculated from colonies in those six plots only. Abundances from all plots in 2004, 2005, and 2006 are presented in Figure 2-3bi.

	Observed Size Range		**Observed Mean Size**		**Abundance**									**Stable Size Distribution**					
Size Class	Min (cm^2)	Max (cm^2)	Mean (cm^2)	SE (cm^2)	'04^{a}	'05^{a}	'06^{a}	'06	'07	'08	'09	'10		'04-5^{a}	'05-6^{a}	'06-7	'07-8	'08-9	'09-10
1	0.2	100	43	1	22	25	28	94	72	66	87	62		0.19	0.37	0.12	0.22	0.37	0.17
2	100	900	369	9	46	49	31	110	93	98	101	93		0.36	0.22	0.23	0.34	0.33	0.26
3	900	4000	2158	49	33	37	21	66	67	60	50	44		0.29	0.14	0.21	0.16	0.13	0.17
4	4000	47,250	11171	405	32	31	22	51	55	65	64	70		0.15	0.27	0.44	0.28	0.17	0.40
				Total	133	142	102	321	287	289	302	269	λ =	1.05	0.71	1.00	1.05	0.97	1.01

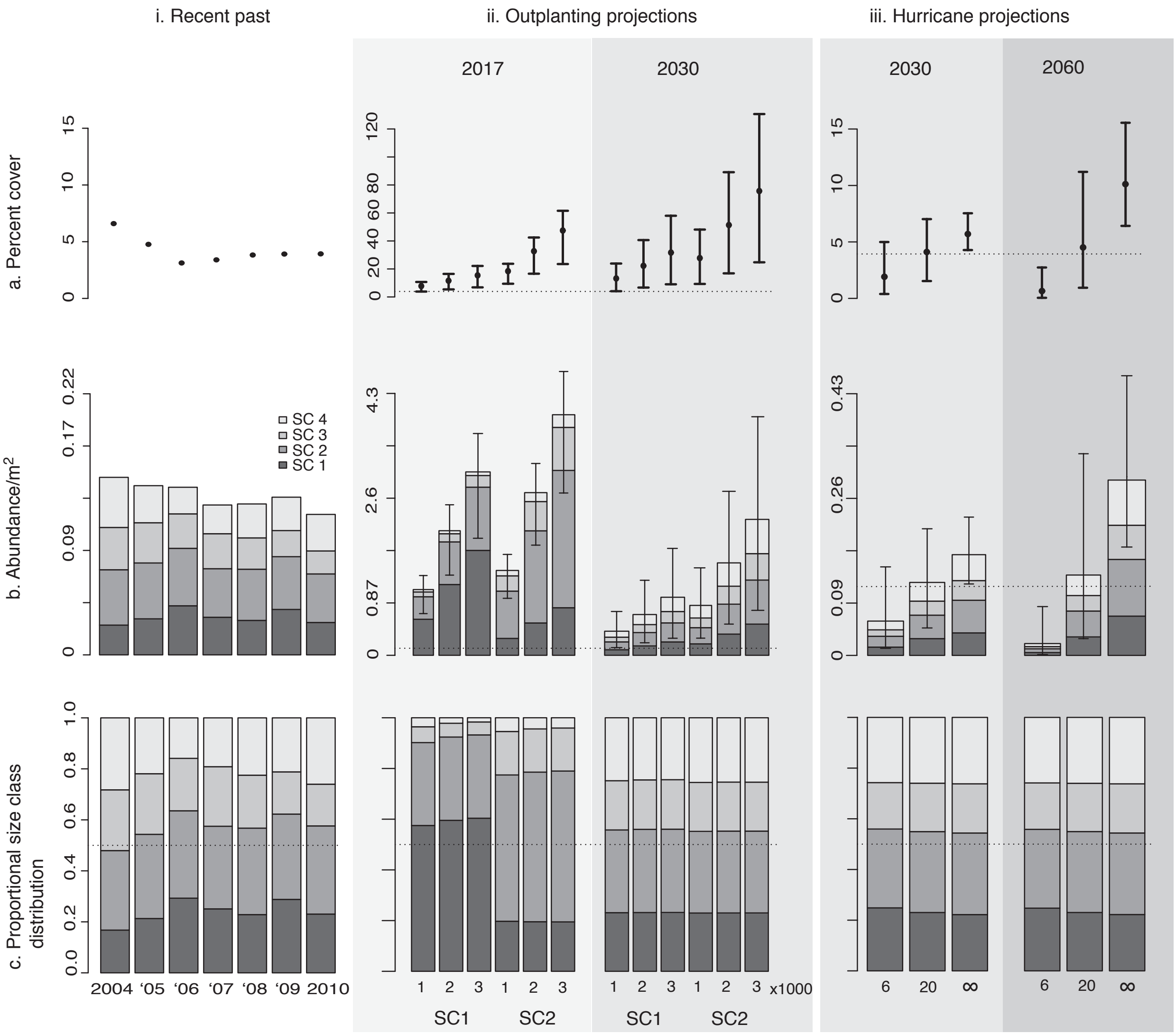


Figure 2-3: Percent cover, density, and proportional size class distribution of *Acropora palmata* are presented in three vertical panels from left to right as follows: (i) as observed over the course of the study from 2004 to 2010 (2005 spring and summer surveys combined), (ii) as projected after five years of outplanting, and (iii) as projected under different hurricane return times: 6, 20, and an infinite number of years. The hurricane scenarios are projected for 20 and 50 years, to 2030 and 2060. The outplanting projections have a two-year lag time with no outplanting, followed by five years of outplanting either size class 1 (SC1) or size class 2 (SC2) outplants at three densities (1000, 2000, or 3000 outplants over the 2300 m^2 study area). Results are shown immediately following five years of outplanting (in the year 2017) and 13 years after the end of outplanting (2030). All results are means based on 10,000 simulations. Error bars represent a 95% confidence interval on percent cover and total abundance. Dotted lines represent percent cover or abundance as measured in 2010, and 50%, in panels (a), (b), and (c), respectively.

(a) **2004–5** [ab]

	1	2	3	4
1	.60	.07	0 +.06	0 +.28
2	.15	.69	.10 +.06	.06 +.30
3	.01	.11	.74	.11 +.23
4	0	0	.11	.83
	.75	**.87**	**.94**	**1**

(b) **2005–6** [b]

	1	2	3	4
1	.44	.14	.08 +.03	0 +.19
2	0	.37	.19 +.03	0 +.16
3	0	.02	.43	.13 + 0
4	0	0	0	.71
	.44	**.53**	**.70**	**.84**

(c) **2006–7** [c]

	1	2	3	4
1	.60	.12	0 +.01	0 +.05
2	.13	.61	.11 +.02	0 +.11
3	0	.12	.79	.04 + 0
4	0	0	.09	.96
	.72	**.85**	**.98**	**1**

(d) **2007–8**

	1	2	3	4
1	.56	.12	0 +.04	0 +.22
2	.24	.67	.07 +.04	0 +.20
3	.01	.06	.70	.07 +.04
4	0	0	.21	.93
	.81	**.85**	**.99**	**1**

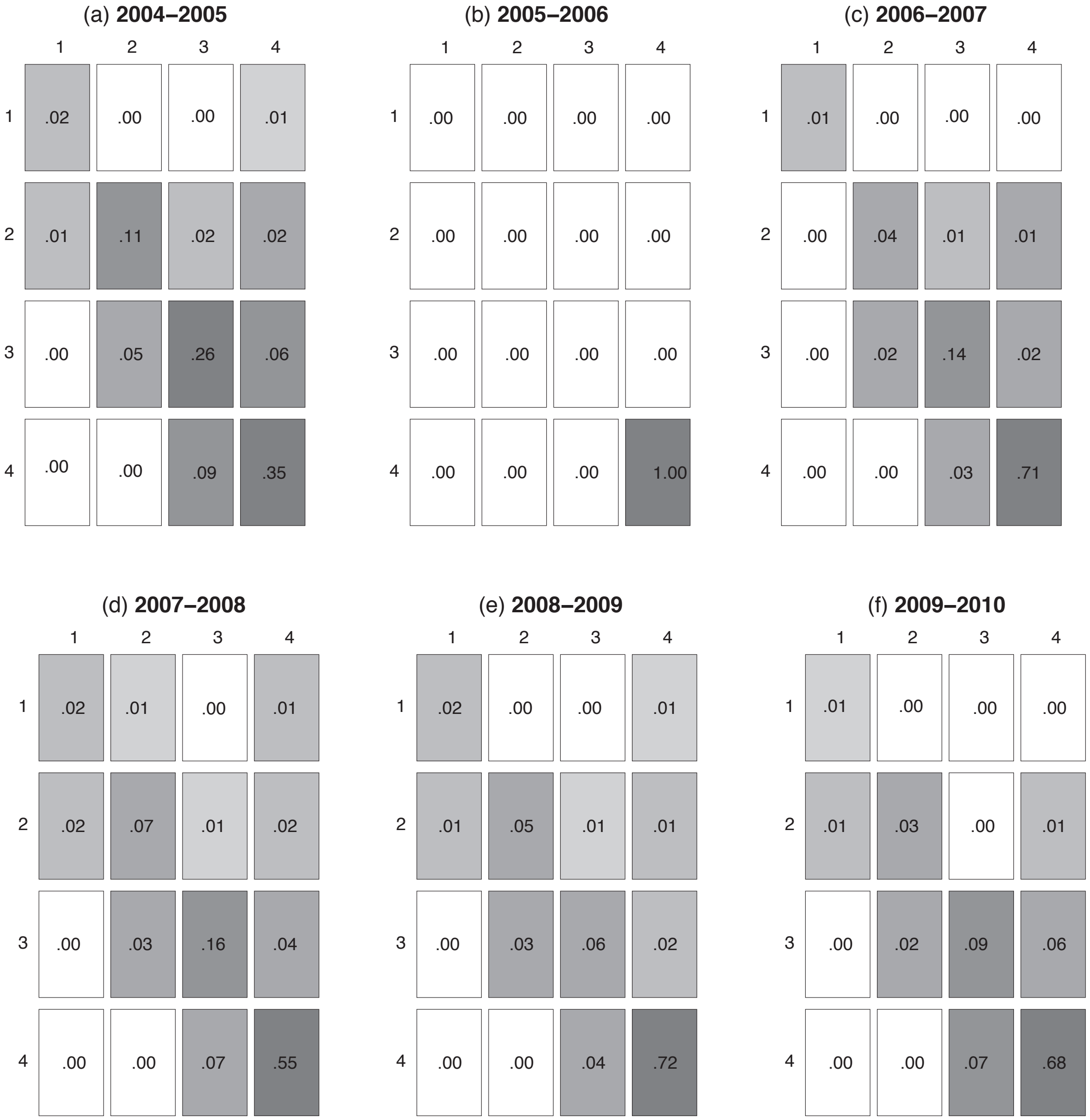
(e) **2008–9**

	1	2	3	4
1	.64	.11	.03 +.09	0 +.41
2	.12	.57	.22 +.06	0 +.31
3	0	.11	.53	.08 +.03
4	0	0	.07	.92
	.76	**.80**	**.85**	**1**

(f) **2009–10**

	1	2	3	4
1	.43	.11	.02 +.03	0 +.15
2	.21	.57	.16 +.02	0 +.12
3	0	.08	.54	.09 +.05
4	0	0	.24	.91
	.63	**.76**	**.96**	**1**

Figure 2-4: Annual population matrices. Each matrix comprises transition and recruitment probabilities, or rates, from one size class (column) to another (row). In columns three and four, the first figure in the sum is the probability of shrinking and the second figure in the sum is the probability of recruiting. For example, in 2007-2008 the probability of a SC3 individual shrinking to a SC2 is 0.07, and the probability of a SC3 giving rise to a new SC2 individual is 0.04. Size-specific survivorship, the sum of transition probabilities not including recruitment, is presented underneath each matrix. [a] Probabilities based on a six-month time interval. [b] Probabilities based on six plots. [c] Recruitment probabilities based on six plots.



(a) **2004–2005**

	1	2	3	4
1	.02	.00	.00	.01
2	.01	.11	.02	.02
3	.00	.05	.26	.06
4	.00	.00	.09	.35

(b) **2005–2006**

	1	2	3	4
1	.00	.00	.00	.00
2	.00	.00	.00	.00
3	.00	.00	.00	.00
4	.00	.00	.00	1.00

(c) **2006–2007**

	1	2	3	4
1	.01	.00	.00	.00
2	.00	.04	.01	.01
3	.00	.02	.14	.02
4	.00	.00	.03	.71

(d) **2007–2008**

	1	2	3	4
1	.02	.01	.00	.01
2	.02	.07	.01	.02
3	.00	.03	.16	.04
4	.00	.00	.07	.55

(e) **2008–2009**

	1	2	3	4
1	.02	.00	.00	.01
2	.01	.05	.01	.01
3	.00	.03	.06	.02
4	.00	.00	.04	.72

(f) **2009–2010**

	1	2	3	4
1	.01	.00	.00	.00
2	.01	.03	.00	.01
3	.00	.02	.09	.06
4	.00	.00	.07	.68

Figure 2-5: Elasticity analyses for annual projection matrices. Values inside the boxes, e_{ij}, are elasticities of population growth rate, λ, for each corresponding value, a_{ij}, in the **A** matrix. Darker colors correlate with higher values for matrix. All projection matrices show that e_{44}, the elasticity of SC4 surviving and not shrinking, has the largest contribution to λ. Because the population growth rate for the 2005-2006 time interval is far from stable ($\lambda < 1$), the elasticity values are extreme.

REFERENCES

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

Acevedo R., J. Morelock, R.A. Olivieri. 1989. Modification of coral reef zonation by terrigenous sediment stress. Palaios 4:92–100.

Adey W.H., P. Adey, R. Burke, L. Kaufman. 1977. The Holocene reef systems of eastern Martinique, French West Indies. Atoll Research Bulletin 218: 1-40.

Adey W.H. 1978. Coral-Reef Morphogenesis - Multidimensional Model. Science 202:831–837.

Bak R., and M. Engel. 1979. Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Marine Biology 54:341–352.

Baums I.B., M.W. Miller, A.M. Szmant. 2003. Ecology of a corallivorous gastropod, *Coralliophila abbreviata*, on two scleractinian hosts. I: Population structure of snails and corals. Marine Biology 150:1215–1225.

Bruckner A., and T. Hourigan. 2000. Proactive management for conservation of *Acropora cervicornis* and *Acropora palmata*: application of the U.S. Endangered Species Act. Proceedigns of Ninth International Coral Reef Symposium 2: 661–666.

Carpenter K.E., M. Abrar, G. Aeby, R.B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortes, J.C. Delbeek, L. DeVantie, et al. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321:560–563.

Caswell H. 2001 Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, MA.

del Mónaco C., N. Noriega, S. Narciso. 2011. Note on density and predation rate of *Coralliophila abbreviata* and *Coralliophila caribaea* on juvenile colonies of *Acropora palmata* in a deteriorated coral reef of Cayo Sombrero, Morrocoy National Park, Venezuela. Latin American Journal of Aquatic Resources 39:161–166.

Doak D., and Morris W. 1999. Detecting population-level consequences of ongoing environmental change without long-term monitoring. Ecology 80:1537–1551.

Edmunds P.J. 2010. Population biology of *Porites astreoides* and *Diploria strigosa* on a shallow Caribbean reef. Marine Ecology Progress Series 418:87–104.

Edmunds P.J., and R. Carpenter. 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proceedings of the National Academy of Sciences 98:5067–5071.

Federal Register. 2010. Endangered and threatened wildlife; notice of 90-day finding on a petition to list 83 species of corals as Threatened or Endangered under the Endangered Species Act (ESA). Federal Register 75:6616–6621.

Fong P., and P.W. Glynn. 1998. A dynamic size-structured population model: does disturbance control size structure of a population of the massive coral *Gardineroseris planulata* in the Eastern Pacific? Marine Biology 130:663–674.

Gardner T.A., I.M. Coté, J.A. Gill, A. Grant, A.R. Watkinson. 2005. Hurricanes and Caribbean coral reefs: impacts, recovery, patterns, and role in long-term decline. Ecology 86:174–184.

Geister J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Proceedings, Third International Coral Reef Symposium: 23–29.

Goreau T. 1959. The ecology of Jamaican coral reefs I. Species composition and zonation. Ecology 40:67–90.

Highsmith R.C. 1982. Reproduction by fragmentation in corals. Marine Ecology Progress Series 7:207–226.

Highsmith R., A. Riggs, C.M. D'Antonio. 1980. Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. Oecologia 46:322–329.

Hubbard D., H. Zankl, I. Van Heerden, I. Gill. 2005. Holocene reef development along the Northeastern St. Croix Shelf, Buck Island, US Virgin Islands. Journal of Sedimentary Research 75:97–113.

Hubbard D., R. Burke, I. Gill, W. Ramirez, C. Sherman. 2008. Coral-reef geology: Puerto Rico and the US Virgin Islands. In: Riegl B, Dodge R (Eds). Coral Reefs of the USA. p. 263–302.

Hughes T.P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. American Naturalist 123:778–795.

Hughes T.P., and J.H. Connell. 1987. Population dynamics based on size or age? A reef-coral analysis. American Naturalist 129:818–829.

Hughes T.P., and J. Tanner. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81:2250–2263.

Holmes G., and R.W. Johnstone. 2010. Modelling coral reef ecosystems with limited observational data. Ecological Modelling 221:1173–1183.

IUCN (International Union for the Conservation of Nature) (2011) The IUCN Red List of Threatened Species. Version 2011.1. Accessed 2 Aug. www.iucnredlist.org

Jackson J.B.C., and T.P. Hughes. 1985. Adaptive strategies of coral-reef invertebrates. American Scientist 73:265–274.

Jackson J.B.C. 1992. Pleistocene perspectives on coral-reef community structure. American Zoologist 32:719–731.

Jackson J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, J.A. Estes, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637.

Kline D., N. Kuntz, M. Breitbart. 2006. Role of elevated organic carbon levels and microbial activity in coral mortality. Marine Ecology Progress Series 314:119–125.

Knowlton N., J.C. Lang, M. Rooney. 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. Nature 294:251–252.

Knowlton N., J.C. Lang, B.D. Keller. 1990. Case study of natural population collapse: post-hurricane predation on Jamaican staghorn corals. Smithsonian Contributions to the Marine Sciences 31:1-26.

Lang J.C., Ed. 2003. Status of coral reefs in the western Atlantic: Results of initial surveys, Atlantic and Gulf Rapid Reef Assessment(AGRRA) program. Atoll Res Bull 496:1-635.

Lirman D. 2000. Fragmentation in the branching coral *Acropora palmata* (Lamarck): growth, survivorship, and reproduction of colonies and fragments. Journal of Experimental Marine Biology and Ecology 251:41–57.

Lirman D. 2003. A simulation model of the population dynamics of the branching coral *Acropora palmata* - Effects of storm intensity and frequency. Ecological Modelling 161:169–182.

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

Miller, M.W. 2001. Corallivorous snail removal: evaluation of impact on *Acropora palmata*. Coral Reefs 19:293–295.

Miller M.W., I.B. Baums, D.E. Williams. 2007. Visual discernment of sexual recruits is not feasible for *Acropora palmata*. Marine Ecology Progress Series 335:227–231.

National Oceanic and Atmospheric Administration. 2011. Historical hurricane tracks. Accessed March 29. www.csc.noaa.gov/hurricanes/#.

Pandolfi J.M., and J.B.C. Jackson. 2001. Community structure of Pleistocene coral reefs of Curaçao, Netherlands Antilles. Ecological Monographs 71:49–67.

Pandolfi J.M., and J.B.C. Jackson. 2006. Ecological persistence interrupted in Caribbean coral reefs. Ecology Letters 9:818–826.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

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

Soong K., and J.C. Lang. 1992. Reproductive integration in reef corals. Biological Bulletin 183:418–431.

Stubben C., and B. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22:1–23.

Williams D.E., and M.W. Miller. 2010. Drivers of population decline in *Acropora palmata* in the Florida Keys National Marine Sanctuary. Linking Science to Management: A Conference and Workshop on the Florida Keys Marine Ecosystem.

Williams D.E., M.W. Miller, K.L. Kramer. 2006. Demographic monitoring protocols for threatened Caribbean *Acropora* spp. corals. NOAA Technical Memorandum NMFS-SEFSC-543.

Williams D.E., M.W. Miller, K.L. Kramer KL. 2008. Recruitment failure in Florida Keys *Acropora palmata*, a threatened Caribbean coral. Coral Reefs 27:697–705.

Williams D.E., and M.W. Miller (*in press*) Attributing mortality among drivers of population decline in Acropora palmata in the Florida Keys (USA). Coral Reefs.

Yee, S. H., D. L. Santavy, M. G. Barron. 2011. Assessing the effects of disease and bleaching on Florida Keys corals by fitting population models to data. Ecological Modelling 222:1323–1332.

Chapter 2, in its entirety, was submitted to Endangered Species Research. Vardi, Tali, Williams, D and Sandin S. The dissertation author was the primary investigator and principal author of this manuscript.

CHAPTER 3: Quantifying surface area of a structurally complex, endangered reef-building coral, *Acropora palmata*

ABSTRACT

Acropora palmata is a critically endangered coral that has formed complex shallow reef habitat in the Caribbean for millennia. Three-dimensional surface area is the most ecologically relevant size measurement for any coral, but due to *A. palmata*'s morphological plasticity, it is not straightforward to quantify. Three-dimensional digital software was used to create digital representations of 14 *A. palmata* colonies from which colony surface area (CSA) was calculated. Using maximum likelihood, linear models relating colony surface area to simple field metrics (length, width, and height) and planar projection were parameterized and compared. While all simple field metrics correlated tightly, planar projection was the best predictor of colony surface area. Parameterizing these relationships enables the translation between current demographic colony-based studies and past and future measures of benthic cover.

INTRODUCTION

The coral *Acropora palmata*, listed as threatened on the U.S. Endangered Species List, was once the main builder of shallow reefs in the Caribbean Sea, and its large branching structure provides essential habitat for numerous fish (Lirman 1999) and countless other organisms. This coral has been well studied genetically (Baums et al. 2005, 2006), ecologically (Rogers and Suchanek 1982, Miller 2001, Lirman 2003, Williams et al. 2008), paleontologically (Lighty and MacIntyre 1982, Jackson 1992, Aronson 2001, Pandolfi and Jackson 2001, Pandolfi and Jackson 2006), morphologically (Gladfelter 2007), and from a disease perspective (Ritchie 2006, Kline and Vollmer 2011). Despite this interest, no standard metric exists for measuring individual *A. palmata* colony size.

Acropora palmata is a large, branching scleractinian coral, one of two acroporids in the Caribbean. The fragile branch tips and rapid growth rates exhibited by the species are adaptations to the dynamic reef flat and fore reefs it inhabits, wherein wave action is strong and storms can inflict severe damage. Once occupying vast areas of shallow reefs throughout the Caribbean, population sizes have been diminished to 10% of their former abundance.

A. palmata's skeleton can expand in three ways: along the substrate (encrusting growth), along branch lengths (growth via azooxanthellate axial polyps), and upward into the water column (vertical growth). Ecological pressures favor different growth strategies at different times. For example, encrusting growth dominates during initial settlement and lesion repair, whereas competition for benthic space favors vertical growth in established colonies (Gladfelter 2007). Such morphological complexity highlights the critical importance of identifying a reliable metric for describing this variable species.

Three-dimensional surface area, or colony surface area (CSA), is the most ecologically relevant size measurement for any coral, as it relates directly to reef accretion and is proportional to both sexual and asexual reproductive output (Soong and Lang 1992). However, due to *A. palmata*'s morphologically plastic architecture, including encrusting, branching, or tabular growth forms (Figure 3-1), this metric is not straightforward to quantify. As such, *A. palmata* size has been approximated by various linear metrics, but the relationship between those metrics and actual surface area has never been determined.

Despite the morphological complexity of *A. palmata*, various *in situ* methods of estimating colony size have been developed. Williams et al. (2006) developed Live Area Index (LAI), the squared average of length, width, and height, where length is the maximum dimension and width is the maximum perpendicular dimension (Figure 3-2). Zubillaga et al. (2007) estimated colony size using maximum diameter (equivalent to Williams's "length") multiplied by colony height. Grober-Dunsmore et al. (2006) used maximum dimension alone (also equivalent to Williams's "length"). In a previous study, the present authors used length and width multiplied by percent live tissue to estimate colony size (see Chapter 2). Each metric relies on at least one linear dimension of colony growth, though the geometric combinations vary. Of particular importance is determining whether systematic distinctions emerge among these metrics.

Before the recent basin-wide collapse of the species across the Caribbean, *A. palmata* formed monocultures across vast areas. The shallows of the reef were referred to as “the *palmata* zone” (Goreau 1959, Geister 1977, Adey 1978). Measuring individual colony size highlights the shift in *A. palmata* population structure. Until recently, the distribution of *A. palmata* was described exclusively by percent cover or areal extent of thickets (*Acropora* Biological Review Team 2005). The lack of a standard metric for describing individual colonies highlights the dramatic distributional reduction of the species. Rather than reflecting surface area, these metrics are a relative measure of size in a given study area and/or over a given time frame. In order to relate current quantification to the past and to plan for future recovery, we need a metric that translates across past measures of colony extent, current demographic studies, and future recovery goals.

The ideal way to obtain data on coral colony size would be to establish a strong correlation between an accurate representation of colony surface area and a simple *in situ* field measurement. Holmes (2008) conducted an *ex situ* study of 75 coral colonies spanning a range of growth forms including both massive and branching morphologies. For all growth forms examined, planar projections were good predictors of detailed measurements of colony surface area as measured with a laser scanner (see Figure 3-1b,h for prototypical examples of what is meant by planar projection). Two other studies have developed *in situ* methods to quantify surface area of live coral colonies using underwater digital photography and three-dimensional image analysis software (Bythell et al. 2001, Courtney et al. 2007). These *in situ* methods were used primarily for massive corals, which are roughly hemispherical, but each study also digitized a few *A. palmata* colonies. Together these approaches (1) demonstrate a method to obtain accurate *in situ* estimation of *A. palmata* surface area, and (2) suggest that planar projection, a simple metric obtained in the field and calculated digitally, may reliably predict colony surface area.

The objective of this study was to evaluate the relationship between *Acropora palmata* colony surface area as estimated by simple field measurements and surface area estimates based on three-dimensional digital representations of individual coral colonies. We evaluated both linear colony measurements (length, width, height) and planar projection (PP, aerial view of two-dimensional surface area) as predictors of colony surface area (CSA) modeled using digital photographs. We found that planar projection is the best predictor of colony surface area, while all linear metrics correlate tightly with CSA. Parameterizing these relationships enables the translation among current demographic colony-based studies, with past and future measures of benthic cover.

METHODS

Acropora palmata is a large, branching scleractinian coral, one of two acroporids in the Caribbean. The fragile branch tips and rapid growth rates exhibited by the species are adaptations to the dynamic reef flat and fore reefs it inhabits, wherein wave action is strong and storms can inflict severe damage. Once occupying vast areas of shallow reefs throughout the Caribbean, population sizes have been diminished to 10% of their former abundance.

A. palmata's skeleton can expand in three ways: along the substrate (encrusting growth), along branch lengths (growth via azooxanthellate axial polyps), and upward into the water column (vertical growth). Ecological pressures favor different growth strategies at different times. For example, encrusting growth dominates during initial settlement and lesion repair, whereas competition for benthic space favors vertical growth in established colonies (Gladfelter 2007). Such morphological complexity highlights the critical importance of identifying a reliable metric for describing this variable species.

Creating three-dimensional digital representations of coral colonies

Thirty-three *Acropora palmata* colonies were photographed for digital reconstruction on the southern, leeward coast of Curaçao in November 2007. Colonies were selected haphazardly based on availability of access from all angles and having a generally arborescent morphology. Each colony was photographed from above and from a minimum of four additional angles in profile (Courtney et al. 2007). All photographs were taken with a Canon Powershot 870 camera calibrated for use with PhotoModeler 6.0.

Digital representations of *A. palmata* colonies were created following the protocol developed by Courtney (2007, personal communication) using the software program PhotoModeler 6.0. From the 33 colonies photographed, 14 were chosen for digital reconstruction based on quality of photographs and to provide a range of colony sizes. For each colony, a minimum of four photographs was used to create a three-dimensional, digital wire-frame model (Figure 3-3). Wire-frame models represent three-dimensional objects using a network of points connected by lines. The set of points is defined by the user. Each point corresponds to a unique place on the coral colony and is referenced in at least three photographs (Bythell et al. 2001, Courtney et al. 2007).

Accuracy of digital representations

Bythell et al. (2001) verified the accuracy of using underwater images to generate wire-frame models with PhotoModeler by modeling objects of known surface area and of varying morphological complexity. They found no significant effect of the camera, underwater housing, or of various issues associated with underwater photography (e.g. refraction, backscatter, and increased absorption) on surface area measurement. Moreover, there was no significant effect of complexity on the tight relationship between modeled and measured surface area.

For any organic form, “true” surface area does not exist. Rather, estimation of surface area is dependent upon and increases asymptotically with increasing resolution of measurement. Using three-dimensional digital representations, resolution increases asymptotically with the number of points used to create a wire frame. To determine the asymptotic point density that corresponds with maximum resolution, Bythell et al. (2001) modeled the same hemispherical coral colony (*Diploria strigosa*) repeatedly, adding points incrementally. A density of 0.25 to 0.4 points cm^{-2} was deemed sufficient to produce an adequate model (Bythell et al. 2001). The accuracy of the surface area modeled using this asymptotic point density was compared with that obtained using the foil method. Foil surface area was consistently 11% greater than photo surface area, for corals of varying levels of complexity (n = 12). Despite the demonstrated lack of effect of complexity on the relationship between modeled and measured surface area for test objects, Bythell et al. (2001) used a higher point density range for *A. palmata* (0.44-0.70 points cm^{-2}) than for corals with a less complex shape.

Courtney et al. (2007) assessed the accuracy of PhotoModeler CSA measurements for *A. palmata* specifically, by comparing modeled surface area with surface area measured with a laser scan (2.5 mm resolution). They demonstrated that 94.1% accuracy was achieved at 0.95 points cm^{-2}. The average point density in our CSA models was 1.50 ± 0.34 points cm^{-2}.

Simple field measurements of colony size

Using a PVC meter stick, we measured length, width, and height in the field. Length was estimated as the maximum linear dimension from a planar view. Width was estimated as the maximum perpendicular dimension, and height was estimated as the maximum distance from the substrate to the top of the colony (Figure 3-2). Planar projection was measured from digital photographs of colonies from a bird's eye view utilizing the image analysis software ImageJ (Image Processing and Analysis in Java, Version 1.44, NIH).

Correlating metrics with colony surface area

The CSA measurements generated by PhotoModeler were compared with six estimates based on the simple colony size measurements: planar projection (PP), length squared (LL), width squared (WW), height squared (HH), length multiplied by width (LW), and the square of the average of length, width, and height (Live Area Index, LAI) (Williams et al. 2006). Single linear metrics (L, W, and H) were squared so that all variables were in the same units (cm^2). We used linear and power function models to describe the best fit, according to maximum likelihood, between PhotoModeler estimates of colony surface area and the six estimates based on field data. Even though a colony with a field metric of 0 would have a CSA of 0, linear models forced through zero were not considered. This is because *A. palmata* exhibits greater variability in morphology at small sizes than at large sizes. Specifically, small *A. palmata* colonies tend to grow more vertically than large colonies. Forcing through zero would remove the intercept of a linear model, thereby over-simplifying the relationship and losing resolution at small sizes (Holmes 2008).

Models were fit with log-transformed field measurements. For example, the linear models correlating PP and LAI to CSA are:

Model 1: $\ln(CSA) = \alpha + \beta * \ln(PP)$, and

Model 2: $\ln(CSA) = \alpha + \beta * \ln(LAI)$.

Models were ranked by their log-likelihood values, and each pair of consecutively ranked models was compared using a Bayesian test (Sandin and Pacala 2005). Here, alternative hypotheses are represented by two different models with the same number of parameters, where

m_1 = poorer fitting model

m_2 = better fitting model

L_{mi} = log likelihood for model i.

If the posterior probability that the poorer fitting model, $2 * [\exp(L_{m2}) / (\exp(L_{m1}) + \exp(L_{m2}))]$, is < 0.05, then m_1 is accepted over m_2.

To examine the relationship between simpler metrics and PP, we traced the planar projection of 28 additional colonies from a different set of *A. palmata* photos taken between 2006 and 2008 in Curaçao. Similarly, we used maximum likelihood estimation to fit models, log-likelihood rankings, and Bayesian tests to relate PP with linear field metrics. Sample size for each of these evaluations was equal to the answer to the great question of life, the universe, and everything: 42 (Adams 1979).

RESULTS & DISCUSSION

Though power models show a better fit to the data at smaller values and have slightly higher R^2 values, linear models and power function models were equally likely for all metrics according to Bayesian tests. Because linear relationships are more parsimonious, only they are shown, one for each metric, with corresponding parameter values (slope and intercept), standard deviation, and likelihood values (Table 2-1).

Planar projection (PP) was the best fit explanatory variable, with a likelihood value of 15 compared with the next highest, 1 for LAI (difference is significant, $p < 0.001$). The relationship between PP and CSA, along with the equation and raw data, are shown in Figure 3-4. The three-metric explanatory variable (LAI) was not significantly better than that with two metrics, LW (likelihood = 0.78, $p = 0.82$). However, the other two metric models (LH and HW) were significantly worse, meaning that LW explain CSA equally well to LAI, but LH and HW do not. This is not surprising considering the biology of *A. palmata*, which maximizes its exposure to sunlight by expanding its planar projection, which in turn would be best approximated by length and width.

The best two-metric model, LW, is significantly more probable than any of the single-metric explanatory variables, and the best single-metric explanatory variable is length (L). Even this model has an R^2 value of 0.93 (Table 2-2). For commonly used field metrics, L, LW, LAI, and PP, we show standard error on the slope and intercept (Table 3-2). This facilitates the translation of one- or two-dimensional field data to three-dimensional colony surface area, allowing the researcher to predict a range of values, incorporating the uncertainty from this study.

Holmes (2008) found linear relationships between PP and CSA for multiple coral growth forms using raw (not log-transformed) data from Pacific corals. The regression model using *A. palmata* raw data (Table 3-3) is more similar to his model for tabular morphology than to branching morphology:

A. palmata (raw data): CSA = 1.69*(PP) + 0.03
Tabular Pacific corals: CSA = 2.47*(PP) + 0.02
Open branching Pacific corals: CSA = 6.16*(PP)

Acropora palmata is generally considered to be a branching coral, but in reality is intermediate between the prototypical branching and tabular morphologies. Compared with many Pacific acroporids, which branch intricately, *A. palmata*'s branching architecture is remarkably simple. Thus it is reasonable that *A. palmata* groups more closely with tabular than with branching forms.

In the analysis relating planar projection to field metrics, we found that planar projection was best predicted by LW, which was a significantly better fit than LL. This is a beneficial outcome for researchers that are interested in converting great quantities of linear field metric data into measures of benthic cover.

Limitations of the study

We present here a linear relationship between two-dimensional surface area as projected onto the benthos, and three-dimensional surface area. The parameters of this linear relationship are based on digital representations created from 14 individual colonies ranging from 15 to 100 cm across. The colonies used to create the digital representations were arborescent, with primarily one “layer” of branches. Representing multiple layers of branches is impossible with the technique we utilized, as one layer of branches hides another from view (see Figure 3-1i). Recall that each point on the digital representation must be referenced in three photographs. Thus we used only single-layer arborescent colonies. If multiple layers of branches were common for all sizes of *Acropora palmata*, this restriction would underestimate the general relationship between field metrics and CSA. However, multiple layers of branches rarely form in colonies less than 100 cm across. Thus, our findings can be applied with confidence over the interval of sizes measured, but we caution against extrapolation (see Table 3-3 for raw data).

Acropora palmata colonies are more variable in their morphology than the colonies chosen for this study. They can be crusts or fragments, and large individuals can be tall with few branches or can contain multiple layers of branches (Figure 3-1j,i). These, however, are the extreme cases. Over 50% of the colonies surveyed in Curaçao are arborescent. Based on field surveys throughout the Caribbean, we estimate that 50-75% of any *A. palmata* stand consists of colonies with the prototypical arborescent morphology of the 14 colonies used to create digital representations. Thus the extreme cases were purposefully excluded from this study. The goal herein was to relate simpler metrics that are easy to collect underwater to the actual amount of *A. palmata* tissue on the reef, a general relationship that could be used across reefs for various purposes.

The uncertainty of the estimation of the intercept (Table 3-2) reflects *Acropora palmata* biology, as the intercept of the linear equation becomes important only at small sizes, close to zero. This is because a small colony could be primarily encrusting, in which case PP would exactly equal CSA, or it could comprise primarily one vertical branch rising from the benthos, in which case PP would be significantly less than, perhaps even half of, CSA. Because small colonies have greater variability in their shape, the relationship between the two variables breaks down near zero. This also explains the negative intercept values for the LAI–PP and LW–PP models (Table 3-1B). Due to the uncertainty of the relationship between CSA and other metrics at small sizes, we emphasize again that the equation should not be extrapolated to sizes outside the range measured (Table 3-3).

The creation of three-dimensional digital representations in PhotoModeler can be accurate to a sub-pixel resolution. Some amount of human and software error are likely, however, as the referencing of points across multiple photographs depends on a visual corroboration of the software's estimations. When points do not match as expected, the user adjusts the point, resulting in a so-called "residual" error. Although we maintained error within the recommendations of the software program, it was not zero. Repeated measurements of the same colony were made to check precision in surface area estimation, but new technology exists to reduce human error, or at least replace it with machine error. Scanning via point clouds using, for example, Microsoft Photosynth or PhotoModeler Scanner, utilizes small differences in the gradation in color photographs to form three-dimensional models. This methodology requires hundreds of overlapping photographs, however, rather than the few photographs used to create the digital representations in this study.

Benefits of the study

There are three distinct benefits of using the relationships, particularly the relationship between planar projection and three-dimensional surface area, derived in this study.

(1) Increased efficiency in the field

Using planar projection (PP) rather than linear field metrics will decrease the amount of time necessary to conduct *Acropora palmata* demographic surveys. The National Oceanic and Atmospheric Administration Southeast Fisheries Science Center (SEFSC) has developed a detailed and comprehensive methodology to conduct these surveys, including linear field metrics and planar photography with a scale bar (Williams et al. 2006). These surveys, begun in Florida in 2004, were used to collect the *A. palmata* demographic data on which Chapter 2 is based. We and others have replicated these methods throughout the Caribbean (see Chapter 4), and new surveys using these methods are planned for the southern Florida Keys and the U.S. Virgin Islands.

These surveys provide an abundance of useful information on the status of this endangered species, including not only size but also the amount, likely timing, and causes of mortality. They are therefore slow to conduct. If size is measured from photographs rather than in the field, cost- and energy-intensive dive time can be reduced substantially. The length of time it takes to measure a colony underwater depends on the size of colony, but an average minimum of two minutes to measure and record colony metrics can be assumed. Most *Acropora palmata* demographic surveys are conducted across three sites, each of which has three replicate plots, comprising a minimum of 12 colonies. Eliminating the need for field measurement and underwater transcription of those data would save a minimum of four hours of underwater time, or two dives per location, and would decrease accidental injuries to fragile branch tips.

(2) Improved accuracy

Using planar projection rather than field metrics improves the accuracy of *Acropora palmata* size estimation. Planar projection has the highest correlation with colony surface area according to both likelihood analysis (Table 3-1) and regression (Table 3-2, Figure 3-4). In addition to the SEFSC surveys, the Atlantic Gulf Rapid Reef Assessment (AGRRA) conducts region-wide surveys for which linear measurements are used to assess coral (not just *A. palmata*) size. These surveys would be more accurate and thus more useful to the coral community at large if planar projection as estimated from photography were used.

(3) Increased ability to scale up

As Holmes (2008) points out, a reliable assessment of surface area can help bridge the gap from small-scale studies on the cellular or polyp level to reef- or even regional-scale studies. On the small scale, because size of polyps is standard (Coates and Jackson 1985), number of gametes can be estimated per colony. Using known (low) rates of sexual recruitment, the rate of successful recruitment as a function of colony size can be approximated. Calcification rates and biomass can also be scaled up, as in Holmes (2008). Though error scales correspondingly, because *Acropora palmata* forms a monoculture, these scalings would be less prone to error than for reefs formed from multiple species.

CONCLUSIONS

We discovered a tight linear relationship between two-dimensional projected surface area and modeled three-dimensional surface area of *Acropora palmata* colonies, as estimated from a digital representation. Hughes, Jackson, and others intuited this relationship in 1980 (Hughes and Jackson 1980). Although this relationship has been shown to be true for all corals examined to date (Holmes 2008), because *A. palmata* is an endangered species, the specific parameters of the relationship are important to estimate, and are presented here for use by both coral reef managers in particular and coral reef scientists in general. Because planar projection is both a more accurate representation of the actual quantity of *A. palmata* on the reef and easier to measure in the field, it should replace the collection of linear field metrics wherever possible. If digital photography is precluded as a field collection method, we discovered that measuring length and width of *A. palmata* colonies provides the next closest approximation of accuracy, and that measuring height does not provide significantly more accuracy. Finally, if underwater field time allows for only one metric to be collected, then that metric should be length.

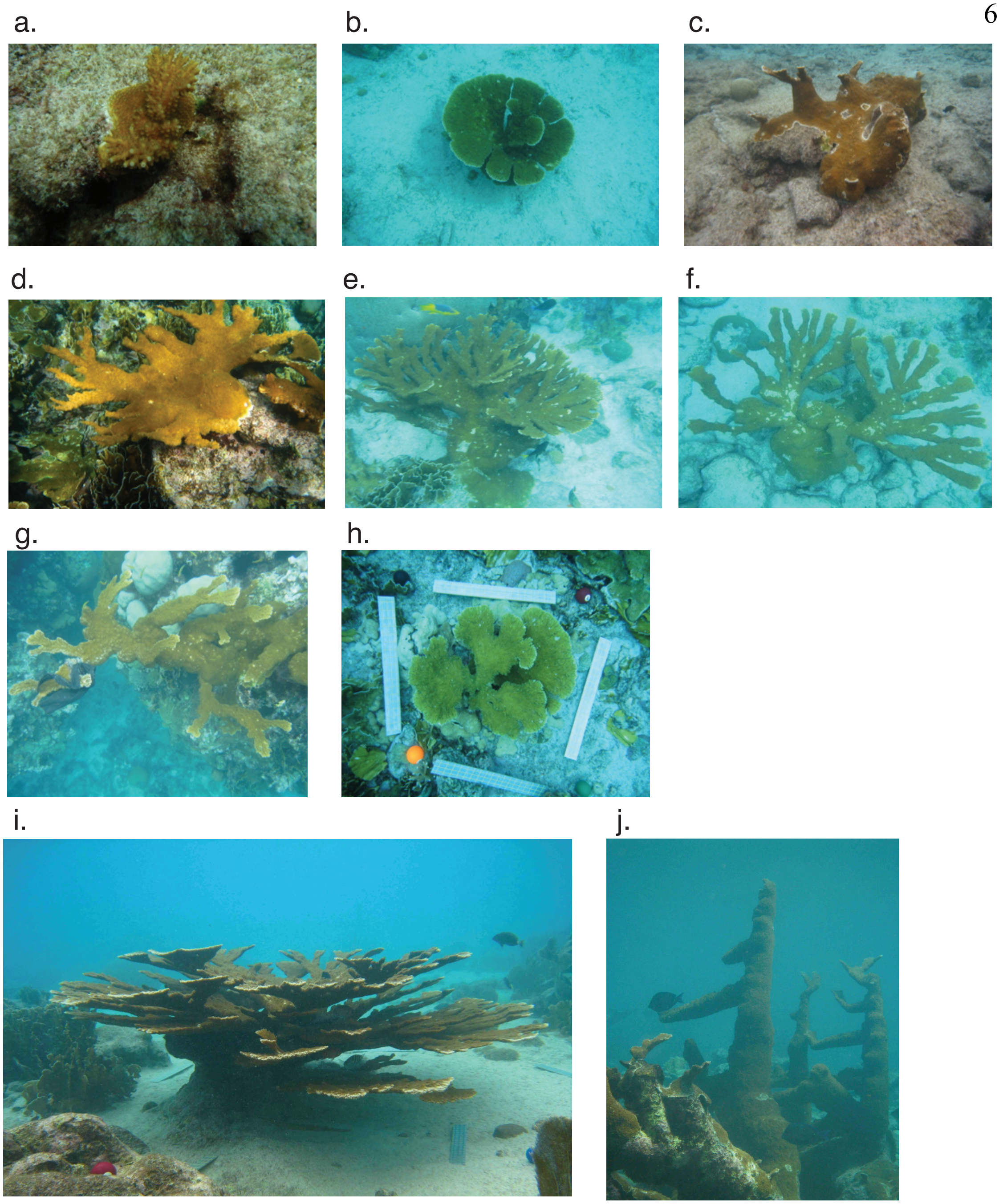


Figure 3-1: Morphological variability of *Acropora palmata.* All photos taken in Curaçao in 2007.

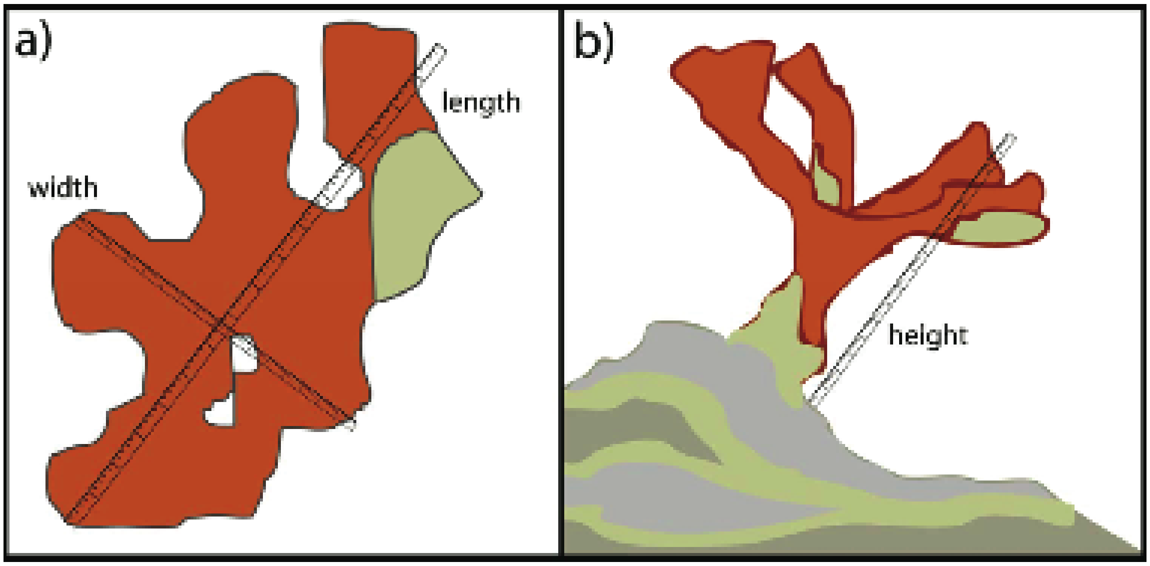


Figure 3-2: Schematic of *Acropora palmata* colony with length, width, and height measurements. Reproduced with permission from Williams et al. 2006.

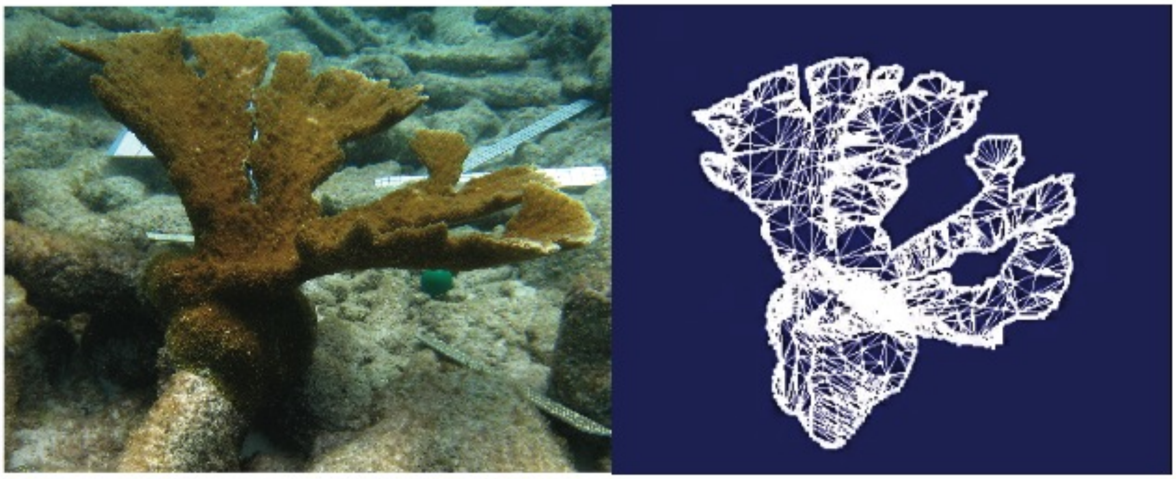


Figure 3-3: Photo of an *Acropora palmata* colony and corresponding image of a three-dimensional wire-frame model.

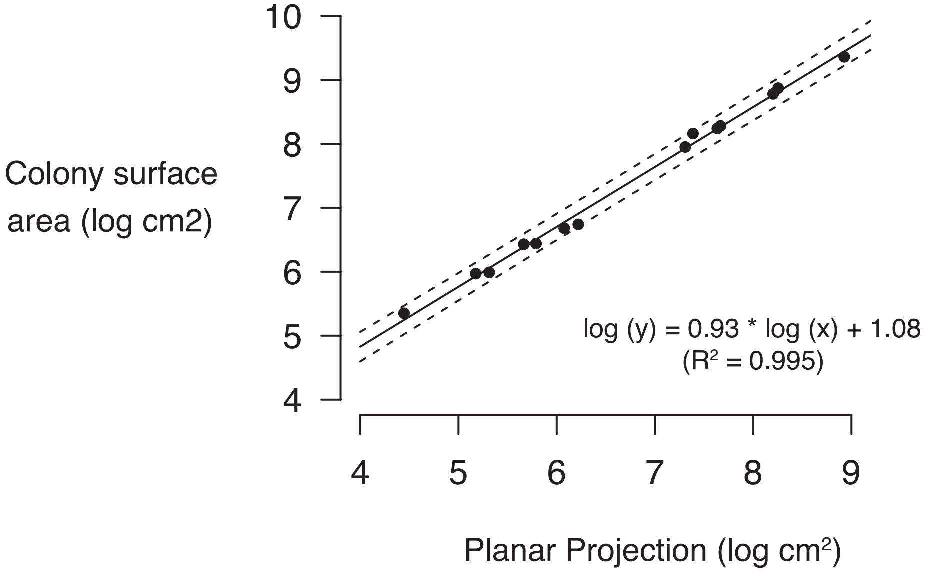


Figure 3-4: Colony surface area (CSA) as a linear function of planar projection (PP) is plotted with its prediction interval. Both data series are log-transformed. The equation of the line is presented.

Table 3-1: A. Intercept, slope, sigma, and log-likelihood values for each of the linear models relating colony surface area to one of eight metrics derived from simple field measurements. Sample size for these analyses is 14. B. Parameter estimates for each of the linear models relating planar projection to simple field measurements. Sample size for these analyses is 42. In each panel, models are ranked according to their likelihood value from best fit to worst, and significant differences between a model and the next best fit are indicated with asterisks (*** = $p < 0.001$, * = $p < 0.05$).

Response variable	Explanatory variable	Intercept	Slope	Sigma	Likelihood
A. Three dimensional surface area					
(n = 14)	Planar Projection	1.08	0.93	0.08	14.87
	LAI	0.83	0.98	0.22	1.14 ***
	L x W	0.46	1.02	0.23	0.78
	L x H	1.21	0.92	0.31	-3.29 *
	L^2	1.04	0.89	0.31	-3.68
	H x W	0.95	1.01	0.34	-4.64
	H^2	1.81	0.89	0.43	-8.20
	W^2	1.02	0.98	0.50	-10.30
B. Planar projection					
(n = 42)	LAI	-0.10	0.97	0.32	-11.30
	L x W	-0.08	0.98	0.33	-13.18
	L^2	0.07	0.92	0.37	-18.35 *
	W^2	0.46	0.94	0.47	-27.93 ***

Table 3-2: Parameter estimates and standard errors for linear models using log-transformed data of the listed explanatory variables. LAI = Live Area Index = the square of the average dimension = (mean (length * width * height))^2. Response variable is colony surface area. SE = standard error as estimated by maximum likelihood. R^2 is calculated from an ordinary least-squares regression.

Explanatory variable	Intercept	SE	Slope	SE	R^2
Planar Projection	1.08	0.12	0.93	0.02	0.995
LAI	0.83	0.33	0.98	0.05	0.965
Length * Width	0.46	0.35	1.02	0.05	0.963
Length^2	1.04	0.45	0.89	0.06	0.929

Table 3-3: Raw field data (length, width, height, and planar projection (PP)) used for fitting log-linear models with colony surface area (CSA) as calculated from digital representations.

Colony #	3DSA (cm2)	PP (cm^2)	Length (cm)	Width (cm)	Height (cm)
1	210	85	15	11	9
2	391	177	15	12	12
3	401	203	18	14	10
4	623	288	20	15	15
5	625	327	20	20	19
6	795	435	26	21	15
7	847	503	19	21	14
8	2,849	1,495	55	23	20
9	3,503	1,617	64	50	40
10	3,806	2,075	50	50	36
11	3,932	2,132	70	28	30
12	6,492	3,649	72	54	43
13	7,112	3,838	100	30	83
14	11,568	7,548	75	70	50

REFERENCES

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.

Adams, D. 1979. The Hitchhiker's Guide to the Galaxy. Page 208. Del Rey, Great Britain.

Adey W.H. 1978. Coral-Reef Morphogenesis - Multidimensional Model. Science 202:831–837.

Aronson, R., and W.F. Precht. 2001. White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460:25–38.

Baums, I.B., M.W. Miller, M.E. Hellberg. 2005. Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. Molecular Ecology 14:1377–1390.

Baums, I.B., M.W. Miller, M.E. Hellberg. 2006. Geographic variation in clonal structure in a reef-building Caribbean coral, *Acropora palmata*. Ecological Monographs 76:503–519.

Bythell, J., P. Pan, and J. Lee. 2001. Three-dimensional morphometric measurements of reef corals using underwater photogrammetry techniques. Coral Reefs 20:193–199.

Coates, A., and J.B.C. Jackson. 1985. Morphological themes in marine invertebrates *in* J.B.C. Jackson, L. Buss, and R. Cook (Eds.). Population biology and evolution of clonal organisms. Yale University Press, New Haven.530 pp.

Courtney, L., W. Fisher, S. Raimonda, L. Oliver, and W. Davis. 2007. Estimating 3-dimensional colony surface area of field corals. Journal of Experimental Marine Biology and Ecology 351:234–242.

Geister J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Proceedings, Third International Coral Reef Symposium 1: 23–29

Gladfelter, E.H. 2007. Skeletal development in *Acropora palmata* (Lamarck 1816): a scanning electron microscope (SEM) comparison demonstrating similar mechanisms of skeletal extension in axial versus encrusting growth. Coral Reefs

Goreau T. 1959. The ecology of Jamaican coral reefs I. Species composition and zonation. Ecology 40:67–90.

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

Holmes, G. 2008. Estimating three-dimensional surface areas on coral reefs. Journal of Experimental Marine Biology and Ecology 365:67–73.

Hughes, T.P., and J.B.C. Jackson. 1980. Do Corals Lie About Their Age? Some Demographic Consequences of Partial Mortality, Fission, and Fusion. Science 209:713–715.

Jackson, J.B.C. 1992. Pleistocene perspectives on coral-reef community structure. American Zoologist 32:719–731.

Kline, D.I., and S.V. Vollmer. 2011. White band disease (type I) of endangered Caribbean acroporid corals is caused by pathogenic bacteria. Scientific Reports 1:1–7.

Lighty, R.G., I.G. MacIntyre, and R. Stuckenrath. 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.

Lirman, D. 1999. Reef fish communities associated with *Acropora palmata*: Relationships to benthic attributes. Bulletin of Marine Science 65:235–252.

Lirman, D. 2003. A simulation model of the population dynamics of the branching coral *Acropora palmata* - Effects of storm intensity and frequency. Ecological Modelling 161:169–182.

Miller, M.W. 2001. Corallivorous snail removal: evaluation of impact on *Acropora palmata*. Coral Reefs 19:293–295.

Pandolfi J.M., and J.B.C. Jackson. 2001. Community structure of Pleistocene coral reefs of Curaçao, Netherlands Antilles. Ecological Monographs 71:49–67.

Pandolfi J.M., and J.B.C. Jackson. 2006. Ecological persistence interrupted in Caribbean coral reefs. Ecol Letters 9:818–826.

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

Rogers, C.S., T.H. Suchanek, and F.A. Pecora. 1982. Effects of hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, US Virgin Islands. Bulletin of Marine Science 32:532–548.

Sandin, S.A., and S.W. Pacala. 2005. Demographic theory of coral reef fish populations with stochastic recruitment: Comparing sources of population regulation. The American Naturalist 165:107–119.

Soong, K., and J. Lang. 1992. Reproductive integration in reef corals. The Biological Bulletin 183:418–431.

Williams, D.E., M.W. Miller, and K.L. Kramer. 2008. Recruitment failure in Florida Keys *Acropora palmata*, a threatened Caribbean coral. Coral Reefs 27:697–705.

Williams, D.E., M.W. Miller, and K.L. Kramer. 2006. Demographic monitoring protocols for threatened Caribbean *Acropora* spp. corals. Page 91 NOAA Technical Memorandum NMFS-SEFSC-543.

Zubillaga A.L., L.M. Márquez, A. Cróquer, and C. Bastidas. 2007. Ecological and genetic data indicate recovery of the endangered coral Acropora palmata in Los Roques, Southern Caribbean. Coral Reefs 27:63–72

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CHAPTER 4: Regional analysis of *Acropora palmata* population dynamics

ABSTRACT

Throughout the Caribbean, the formerly dominant shallow-reef building coral, *Acropora palmata*, exists at 5-10% of its former abundance. Based on two- to eight-year data sets from six locations across the region, we parameterized population dynamic rates using matrix modeling with demographic stochasticity. We found that the decline in abundance is projected to continue, though there are regional differences. Only in Jamaica, which has experienced no significant storms in 30 years and has an order of magnitude more sea urchins than elsewhere, is *A. palmata* increasing in both percent cover and abundance.

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INTRODUCTION

Coincident with the closing of the Isthmus of Panama, *Acropora palmata* evolved in the Pliocene, two to three million years ago (Budd and Johnson 1999). For the past 500,000 years it has formed the shallow reefs of the Caribbean, keeping pace with sometimes rapid sea level rise throughout the Pleistocene and Holocene (Greenstein et al. 1998, Jackson et al. 2001). Although still present throughout its range (Lang 2003), populations are at less than 10% of their former abundance (*Acropora* Biological Review Team 2005). This is alarming because a rapid decline in *A. palmata* is unprecedented in the fossil record (Wapnick 2004, Pandolfi and Jackson 2006).

Acropora palmata has evolved unique traits to inhabit the dynamic shallow zones of the reef – the reef flat and upper reef crest. These adaptations are: rapid growth (with the cost of a relatively weak skeleton) (Jackson and Hughes 1985), dependence on wave action for sloughing off sediment (Rogers 1983), and a plastic morphology to facilitate regrowth in any direction (Gladfelter 2007). These traits lead to the competitive exclusion of virtually all other corals in Caribbean shallow reefs from 0-5 m. Because there is no functional redundancy, the impending extinction of this species is a pressing conservation concern. With its large, complex, branching architecture, *A. palmata* has created and maintained shallow reef habitat and slowed shore-bound wave energy for millennia. Its disappearance assures population reductions for untold numbers of invertebrates and fish (Lirman 1999).

White band disease has been targeted as the proximal cause of this decline in abundance (Aronson and Precht 2001); however, disease prevalence is patchy, and it is often misdiagnosed (Williams et al. 2006). Thus, there are still a multitude of unanswered questions regarding the sudden decline in extent of such a formerly pervasive and persistent organism. Are all populations decreasing at the same rate? Are some populations increasing? Are there geographic patterns to this population collapse?

Despite the high profile of this threatened species and its critical role in creating reef habitat, little is known about regional differences in population dynamics. We chose three locations in the Caribbean to study these potential differences: Curaçao, Florida, and Jamaica. The three locations and the differences in their *Acropora palmata* population status are described below.

Curaçao

The island of Curaçao, formerly of the Netherlands Antilles, lies off the north coast of Venezuela and harbors some of the southernmost reefs in the Caribbean. In Curaçao, *A. palmata* grows out of the wide beach flat preceding the reef slope, oftentimes growing directly out of the sand. Curaçao is below the hurricane belt (Bries et al. 2004) and has long periods of meteorological stability (notable exceptions include Hurricanes Lenny in 1999 and Omar in 2008). Long intervals between major storms allow time for the development of *A. palmata* thickets, or at least for a relatively high proportion of large individuals (van Duyl 1985, Woodley 1992).

Florida

The Upper Florida Keys represent the northern range limit for *A. palmata*. This area is one of the most visited coral reefs in the world, experiences a high frequency of hurricanes relative to the rest of the Caribbean (Gardner et al. 2005), has suffered from a century of overfishing (McClenachan 2009), and is severely degraded (Pandolfi et al. 2005). The Florida Keys are a barrier reef system. Currently *A. palmata* is found as individual colonies almost exclusively on the tops of spurs in the spur-in-groove system offshore of the Upper Keys – an area that formerly housed luxuriant thickets (*Acropora* Biological Review Team 2005).

Jamaica

Jamaica is one of the best-studied reefs in the Caribbean and is severely overfished (Jackson 1997). The reefs of much of the northern coast were demolished by the Category 5 Hurricane Allen in 1980 (Woodley et al. 1981). They then succumbed to dominance by macroalgae after the sole remaining herbivore, the sea urchin *Diadema antillarum*, disappeared in 1983 (Lessios et al. 1984, Hughes 1994). *Diadema antillarum* is now recovering in Jamaica (Edmunds and Carpenter 2001) and appears to be paving the way for *A. palmata* to resume building the reef.

These three locations were chosen to highlight potential differences in *Acropora palmata* population dynamics. For example, in Curaçao, where storms are infrequent, we suspected growth rates to be larger than shrinkage rates. Because in Jamaica *A. palmata* appears to be in the early stages of recovery, we anticipated rates of change in population size to be positive and larger than those in the other locations. We asked the following questions: Do *A. palmata* population dynamics differ among these locations? If so, at what spatial scale? Do rates of change in population size or size distributions differ among locations? And finally, how do any potential differences scale with time: What is the projected benthic cover in 20 years? In 90 years?

We used matrix population modeling to evaluate these questions, and we contextualized our findings with results from more limited data sets for Navassa, Puerto Rico, and Virgin Gorda in the British Virgin Islands. Analyzing population dynamics, while keeping in mind the distinct suite of environmental conditions in each of the three primary location, helps to illuminate the drivers behind *A. palmata* dynamics.

METHODS

Study sites and survey frequency

Six locations were selected to study *Acropora palmata* demography across the Caribbean Sea: Curaçao (CUR), the Upper Florida Keys off Key Largo (FL), the northwest coast of Jamaica (JAM), Navassa (NAV), Puerto Rico (PR), and Virgin Gorda in the British Virgin Islands (VG). Demographic surveys were conducted in a hierarchical sampling framework. Two to five sites were sampled at each location for a total of 18 sites (see Figure 4-1). Three 7 m radius plots were surveyed at 13 sites, while the remaining five sites were comprised of one, two, or five plots (see Figures 4-1 and Table 4-A4). Plots were chosen to have a mid-range density of approximately 0.1 *A. palmata* colony m^{-2}. Thickets and areas with sparse solitary colonies were purposely avoided to facilitate initial identification and efficient long-term tracking of individuals over time.

Surveys were conducted at least two times per location, with each survey completed in less than one month (except for the 2010 survey in Puerto Rico, which was conducted over three months). Surveys were conducted approximately annually in three locations (with season and years of surveys in parentheses): Florida (spring, 2004-2011), Curaçao (spring, 2006-2011), and Jamaica (fall, 2007-2010).

At three locations, only two surveys were conducted (with dates of surveys in parentheses): Navassa (fall 2006, spring 2009), Puerto Rico (fall 2007, summer 2010), and Virgin Gorda (winter 2006, fall 2007) (Figure 4-A1).

During each survey, every colony of *A. palmata* within each plot was identified and measured. For each colony, maximal diameter, maximal perpendicular diameter, and percent live tissue were measured *in situ*. Using plot-specific maps, survivorship and growth of individual colonies were estimated. New fragments (those not found in previous surveys) that were attached to the substrate were defined as recruits and were measured and recorded.

In order to use matrix-based methods of analysis, continuous measures of coral size were binned into four size classes as follows: size class 1 (SC1) ≤ 100 cm^2, size class 2 (SC2) ≤ 900 cm^2, size class 3 (SC3) ≤ 4000 cm^2, and size class 4 (SC4) > 4000 cm^2. These size classes have an average diameter (assuming an approximately circular morphology) of 7, 20, 45, and 100 cm, respectively. Only individuals in SC3 and SC4 were assumed to contribute to new colony formation via either sexual recruitment or asexual fragmentation, which were not distinguished. For more details on matrix model formulation, see Chapter 2 Methods and Figure 2-1.

A size-based matrix population model, **A**, is the sum of two component matrices, **T**, the transition matrix, and **F**, the fragmentation matrix (Figure 2-1). Each cell of the transition matrix, t_{ij}, is the number of individuals transitioning from size class j to size class i, divided by the number of individuals in j. The fragmentation matrix is akin to the fertility matrix in standard matrix population modeling terminology (Caswell 2001). The alternate terminology is used because *Acropora palmata* reproduces primarily via fragmentation rather than sexual recruitment. Entries in the fragmentation matrix, f_{ij}, are based on the number of new individuals that arrive in the study area during a specified time interval. New fragments are assumed to arise from the existing stand of colonies and can be of any size class, even SC4. New SC3 fragments are assumed to derive solely from pre-existing SC4 colonies. New fragments of SC1 and SC2 were assumed to derive from existing SC3 and SC4 colonies proportionally, based on the ratio of mean size of SC4 colonies to that of SC3 at the beginning of the time interval. (See Chapter 2 Methods for equations.)

In each of the six locations, rate of change in population size without recruitment, λ_T, was calculated. The total rate of change in population size, λ_A, was calculated by adding recruitment to the survivorship matrix. Note that recruitment was not recorded in Virgin Gorda, so the total rate of change was not calculated for this one location. All matrices and λ values are in Tables 4-1, 4-2, 4-A1, 4-A2, and 4-A3. Stable size class distributions, the right eigenvector of **A** (**T** for Virgin Gorda) are also calculated and presented (Figure 4-4).

Log-linear analyses

Does site matter?

We were interested in determining whether sites within locations differed significantly from one another or whether they were similar. If sites were deemed similar, then they could be grouped together and called representative of a location. Using **T** matrices from each site, we built two linear models for each location. One model included the effects of all possible factors and their interactions (starting size class, ending fate, site and year of transitions). The other excluded site effects. If site effects are significant, then the first, fully parameterized model will fit the data better than the second, under-parameterized model.

In each location, matrix models were parameterized for each survey interval (from one survey to the subsequent) by combining measurements from all sites (usually three sites) within a single location (island). To test the assumption that transition counts for each site within a location behave similarly, we used log-linear analysis, adding 0.5 to avoid log(0) (as in Caswell 2001). For each location, a log-linear model was written in terms of four factors: initial state or size class (*S*); ending fate, including death, growth, or shrinkage to another size class (*F*); site (*X*); and time (*T*). The probability that an individual starts at state *i*, location *k*, and time *l* and ends up with fate *j* is the product of the probabilities that define those variables. The logarithm of the sum of individuals with particular starting and ending conditions is the sum of the effects of these variables (Caswell 2001). Thus, the saturated model can be written:

FSXT: $$\log m_{ijk} = u + u_{S(i)} + u_{F(j)} + u_{X(k)} + u_{T(l)} + u_{SF(ij)} + u_{SX(ik)} + u_{ST(il)} + u_{FX(jk)} + u_{FT(jl)} + u_{XT(kl)} + u_{SFX(ijk)} + u_{SFT(ijl)} + u_{SXT(ikl)} + u_{FXT(jkl)} + u_{SFXT(ijkl)}\,.$$

The model excluding all *X* and *F* interactions is

FST, SXT: $$\log m_{ijk} = u + u_{S(i)} + u_{F(j)} + u_{X(k)} + u_{T(l)} + u_{SF(ij)} + u_{SX(ik)} + u_{ST(il)} + u_{FT(jl)} + u_{XT(kl)} + u_{SFT(ijl)} + u_{SXT(ikl)}\,,$$

where

m_{ijkl} = the number of individuals in state i from location k at time l ending with fate j,

u = the log of the total number of observations in each table,

$u_{S(i)}$ = the effect of the ith state, and

$u_{SF(ij)}$ = the effect of the interaction of the ith state and the jth fate,

and so on.

For each location each pair of models is parameterized using maximum likelihood and compared using a goodness-of-fit test where:

$$G^2 = 2 * \sum_{cells} (\text{observed}) * \log \left(\frac{\text{observed}}{\text{expected}}\right)$$

Does location matter?

To test the hypothesis that the difference among populations from various locations was significant, we employed log-linear analysis, again relying on the original count data (i.e. the number rather than the proportion of individuals transitioning from one size class to another, including the number transitioning to a death class). Each location is described by a table with four columns (size classes 1-4) and five rows (size classes 1-4 plus death). Factors for the model discerning the location effect are similar to those described for the previous model discerning site effects. Time, however, is discounted, as we compared each location over a similar time frame – generally, 2007-2010, though Navassa data were collected from 2006-2009, see Figure 4-A1 for sampling schedule, Virgin Gorda was excluded from this analysis, as data were collected there over a much shorter time frame. Factors for this model were: initial state or size class (*S*); resulting fate, including death, growth, or shrinkage to another size class (*F*); and location (as opposed to site) (*L*). The null hypothesis was that the under-saturated model (FS, SL), which excludes interactions of location on fate, is sufficient to describe observed transitions. The alternate hypothesis is that the fully saturated log-linear model (FSL) is necessary to parsimoniously describe the observed data.

The null, or saturated, model and the model eliminating location and fate interactions are thus

FSL: $\log m_{ijk} = u + u_{S(i)} + u_{F(j)} + u_{L(k)} + u_{SF(ij)} + u_{SL(ik)} + u_{FL(jk)} + u_{FSL(ijk)}$, and

FS, SL: $\log m_{ijk} = u + u_{S(i)} + u_{F(j)} + u_{L(k)} + u_{SF(ij)} + u_{SL(ik)}$, respectively.

G^2 is distributed as X^2 with degrees of freedom equal to the increment in degrees of freedom in the two models ($df = 64$).

To further understand the relationship among locations, we conducted post-hoc, pairwise comparisons among all five locations with comparable survey intervals. For each pair of locations we compared the saturated model (FSL) with the model excluding fate and location interactions (FS, SL). Goodness-of-fit was calculated as above.

Comparison of lambda and percent cover across locations

For deterministic analyses, population growth rate is estimated by the dominant eigenvalue, λ, of a population matrix. Where the transition and/or fragmentation rates comprising a matrix were estimated over a one-year interval, λ represents the annual population growth rate, λ_1. Where two surveys were conducted at some other time interval, x, where x is greater than or less than 1, the dominant eigenvalue is an estimate of the population growth rate over that time interval, λ_x, and $\lambda_1 = \lambda_x^{1/x}$. When projecting abundance for a population that has been parameterized over a non-annual time interval, the number of iterations for the projection was equal to the most recent survey year (e.g. 2010) subtracted from the target year (2030 or 2100) divided by x.

To facilitate direct comparison of the response variables, λ and percent cover, across locations, the mean **T** and **F** matrices were calculated for locations with more than two surveys (Curaçao, Florida, and Jamaica). The mean transition matrix, $\mathbf{T_m}$, has dimensions equal to those of **T**, wherein each element t_{ij} is the arithmetic mean of the corresponding t_{ij} from each annual matrix, and likewise for $\mathbf{F_m}$. Then $\mathbf{A_m} = \mathbf{T_m} + \mathbf{F_m}$. In Curaçao, Florida, and Jamaica, five, seven, and three matrices were averaged, respectively. These mean matrices provide an approximation of the dynamics over the study period.

Projections

We projected population abundance until the years 2030 and 2100 using a variation of the basic matrix population modeling equation,

$$n_{t+1} = \mathbf{A}\, n_t \text{, or}$$

$$n_{t+1} = [\mathbf{T} + \mathbf{F}]\, n_t$$

where n is the population vector comprising number of individuals in size classes 1-4.

Right-multiplying a matrix by the population vector n_t as above results in a deterministic calculation of the population vector at a subsequent time step. For example, if $a_{\mathrm{ij}} = 0.4$ and there are 10 individuals in size class *j* at time *t*, size class *j* will contribute exactly four individuals to size class *i* at time $t + 1$. To incorporate inter-individual variation, we interpreted each column vector, *j*, of the transition matrix, **T**, as a multinomial distribution of probabilities. Thus, if $t_{\mathrm{ij}} = 0.4$, the number of individuals at $t + 1$ is a random variable that has a 0.4 probability of moving from size class *j* to *i* and a 0.6 probability of dying or transitioning to a different size class. Entries in the **F** matrix are assumed to come from a Poisson probability distribution, with $\lambda = f_{\mathrm{ij}}$ (here λ is equal to the expected value of the Poisson distribution, not the population growth rate).

A single iteration of a projection involves the following steps:

- Create a transition matrix, $\mathbf{T_d}$, that accounts for mortality.

$$\begin{matrix} t_{11} & t_{12} & t_{13} & t_{14} \\ t_{21} & t_{22} & t_{23} & t_{24} \\ t_{31} & t_{32} & t_{33} & t_{34} \\ t_{41} & t_{42} & t_{43} & t_{44} \\ t_{m1} & t_{m2} & t_{m3} & t_{m4} \end{matrix}$$

where, t_{ij} = the probability of a SC*j* individual transitioning to SC*i*

$t_{mj} = 1 - \sum t_j$

- Transform each $\mathbf{T}_{\mathbf{dj}}$ into a cumulative probability distribution that sums to 1, where each column is t_j.
- State the current (most recent) population vector, $n = n_1, n_2, n_3, n_4$. For each n_j, create a list of random numbers between 0 and 1, equal in length to n_j, and distributed according to t_j.
- Sum the random numbers in each interval of t_j.
- Take n_3 Poisson draws for each of f_{13} and f_{14} and n_4 Poisson draws for each of f_{i4}.
- Sum the number of new fragments.
- Sum the number of transitions and the number of new fragments into each size class. This is the new population vector, n_{t+1}.
- Divide the sum of the new population vector by the sum of the previous population vector, n_t. This is the annual rate of change in population size, λ_1.
- Choose a target year, t_{max}. For each location, each of the above steps is repeated for the number of iterations necessary to reach t_{max}.
- Take the geometric mean of all λ_1 values > 0.
- Multiply the population vector n_{max} by the mean size for each size class as measured during the study period. Sum those values and divide by the total study area to obtain an estimate of percent cover of *Acropora palmata* on the benthos.
- Repeat the above steps 10,000 times.
- Report the mean and 95% confidence interval for λ and percent cover.

RESULTS

The relative abundance of size classes 1-4 illustrates annual dynamics at each location (Figure 4-2). Through time, the most general pattern of change was a disproportionate reduction of larger size classes in location-years exposed to significant storms. In three locations, CUR, FL, and PR, the abundance of the two largest size classes decreased relative to the abundance of the smallest two size classes directly following years with significant storms. In the three locations that did not experience appreciable storm activity, abundance of the larger, reproductive size classes (SC3 and SC4) increased relative to that of the smaller size classes (SC1 and SC2) over the course of the study.

The same qualitative results can be seen when size data are plotted as a continuous rather than a categorical variable (Figure 4-3). The majority of colonies experienced little to no change in size, as evidenced by the preponderance of points lying along the 1:1 diagonal line, with some evidence of increased shrinkage during storm years. Importantly, patterns of reduction in colony size were size-specific, with smaller colonies more likely to lose a larger proportion of their entire size compared with larger sizes (as evidenced by higher variance in the log-log plot at smaller starting size classes in Figure 4-3). Note that only size change of survivors is reported here, with details of whole-colony mortality described along with the matrices below.

Matrices

Direct spatial comparison of transition and fragmentation rates was conducted in one approximately three-year window from 2007 to 2010 across five locations:

Curaçao, Florida, Jamaica, Navassa, and Puerto Rico (Table 4-1). Virgin Gorda was assessed for a more limited 1.75-year period. As assessed over the three-year time period, Jamaica and Florida exhibited positive rates of change in population size ($\lambda_3 > 1$), while Curaçao and Puerto Rico exhibited negative rates of change in population size. This division is correlated with storms, as the *A. palmata* populations in Curaçao and Puerto Rico experienced significant storm damage during this interval, while the Jamaica and Florida populations did not. In Navassa, due to limited sampling, there were no observed transitions between SC1 or SC2 to SC3 or SC4. As such, the **T** matrix operates as two separate sets of equations. Further, no mortality was observed in either of the larger two size classes, thereby creating an artificial "eternal" population of larger colonies. Thus, the long-term solution of λ_T is exactly equal to 1.00 (without any rounding). In matrix **A**, adding fragmentation from SC3 and SC4 changes the stable size-class distribution, but since there is no feedback between recruitment and densities of SC3 or SC4, the long-term population growth with recruitment, λ_A, is also exactly 1.00.

In all locations, mortality decreased with increasing size class (0.57 ± 0.12, 0.46 ± 0.09, 0.27 ± 0.10, 0.19 ± 0.09; mean ± SE for size classes 1-4, respectively), meaning that small individuals have a higher probability of whole-colony mortality than large individuals; in other words, mortality scales with size. In Curaçao and Puerto Rico, mortality rates were greater than all other rates for all size classes, and the same was true for size classes 1-3 in Puerto Rico. Stasis (no change in size class) also scales with size class in most cases. Stasis of SC4 was highest among all nonmortality transitions. We know from elasticity analyses that perturbations to t_{44} have the largest effect on λ (Chapter 2).

Patterns of fragmentation were assumed to be size-specific, with larger colonies producing more fragments than smaller colonies. In general, across locations the highest rate of fragmentation was from SC4 to SC2 (range 0.17-0.95). Jamaica and Curaçao had the highest rates of fragmentation for the largest size class, with close to one new SC2 fragment produced annually for each existing SC4 individual ($f_{42} = 0.95$ and 0.90, respectively).

Purely spatial comparisons of population trajectories for the three-year window from 2007-2010 were confounded by temporal patterns of storm activity, with the locations suffering significant storm activity during this window (Curaçao and Puerto Rico) showing the highest rates of population decline. To examine whether the spatial division was due to a characteristic difference in dynamics or simply a difference between populations disturbed and undisturbed by storms, we removed time intervals during storms (2008-2009 in Curaçao, 2004-2005 and 2005-2006 in Florida) and averaged the remaining matrices (four in Curaçao and five in Florida) to generate one characteristic annual matrix. The result is a mean "calm years" matrix for each location. The results of removing time intervals with significant storm activity from the calculation of mean matrices in Curaçao and Florida are mixed (Table 4-2). Florida had a $\lambda < 1$ when storms were included ($\lambda = 0.961$) and a $\lambda > 1$ when storms were excluded (2004-2005 and 2005-2006 matrices excluded, $\lambda = 1.081$). In Curaçao, λ increased but remained below one ($\lambda_{all\ years} = 0.910$, $\lambda_{calm\ years} = 0.959$). Annual population growth rates for all locations were much more comparable when excluding data from storm years (Table 4-2).

Analyses of annual matrices (Table 4-2) reveal comparable patterns as three-year matrices, though tendency towards stasis is predictably more pronounced. Growing more than one size class during a single year occurred only twice (both instances in Jamaica) (Table 4-A3). Unlike in the three-year matrices, where mortality was the highest transition rate for all size classes in Curaçao, for SC1 through SC3 in Puerto Rico, and for SC1 and SC2 in Jamaica and and Florida, the greatest transition rate in the annual matrices was stasis for all size classes in Florida and in all but SC1 for other locations.

Stable size distributions

Stable size-class distributions (SSDs) for Curaçao, Florida, Jamaica, Navassa, Puerto Rico, and Virgin Gorda are presented in Figure 4-5. SSDs present the ultimate distribution of size classes 1-4, for each location, assuming dynamics do not change. Curaçao and Florida afford a comparison of SSDs estimated during calm and storm years. In both locations, the SSDs estimated from storm years are characteristically different than SSDs from non-storm years. Specifically, storm year dynamics predict dominance by SC1 and SC2. The relative proportion of these size classes combined was 0.75, 0.94, and 0.79, for Curaçao 2008, Florida 2004, and Florida 2005, respectively. Dynamics during calm years predict a more equivalent distribution between small and large individuals. The SSD based on the mean matrix for each location predicts the relative proportion of SC1 and SC2 to be 0.49 in Curaçao and

0.63 in Florida. These numbers match almost exactly the relative proportion of SC1 and SC2 individuals in the most recent survey in each location (0.49 and 0.61, respectively), indicating that the current population is likely near its stable size-class distribution.

The data from multiple years from Florida and Curacao offer important insights into the prominence of environmental stochasticity in these data. The variability in SSDs among years suggests that interannual variability of transition matrices has appreciable influential on long-term dynamics (as shown by Hughes 1984), and results from locations with two surveys should be interpreted as snapshots rather than comprehensive characterizations of those populations' long-term dynamics.

Log-linear analyses

Site effect within locations

We used goodness-of-fit to test the null hypothesis that site within each location was an important factor explaining difference in number of transitions from a particular state to a particular fate through time. The null hypothesis was that the effects of site on fate do not help explain the data; in other words, that an under-saturated model (FST, SXT), which excludes all interactions of site on fate, is sufficient to describe observed transitions. The alternate hypothesis is that the fully saturated log-linear model, termed FSXT and including all interactions among state, fate, site, and time, is necessary to parsimoniously describe the observed data, thus suggesting a significant effect of site on transition probabilities.

For all locations, there was insufficient support to reject the null hypothesis, suggesting that accounting for the different sites within each location does not significantly improve the power of explanation over a model that lumps sites together (Table 4-3). The most support for rejection (though still not significant) was observed for Puerto Rico, where one site, La Cordillera, was 190 km from the other two sites (in contrasts to distances ranging from 2 to 30 km for other sites within locations). The results from this test suggest that variability among sites within a location was limited.

Location effects across the Caribbean

Similarly, we used goodness-of-fit tests with log-linear models to test whether location is an important factor explaining the difference in transition count matrices (Table 4-4). Comparing transition matrices across the same time period (2007-2010) for all locations except Virgin Gorda, we found significant effects of location, suggesting that the five locations examined are characteristically different from one another, or that variability among transition counts is not homogenous at the regional scale (Table 4-4.A). All locations contributed significantly to the location effect with the exception of Puerto Rico, which was statistically indistinguishable from the "consensus" matrix (Table 4-4B).

To examine any potential groupings we conducted a post-hoc pairwise comparison of the goodness-of-fit of the FSL and FS, SL log-linear models among pairs of locations. (Table 4-5). All pairwise comparisons revealed significant differences, with the exception of Curacao vs. Jamaica and Florida vs. Navassa. We may summarize the matrix comparisons as follows: CUR, JAM ≠ PR ≠ FL, NAV.

Differences in matrices may be linked to at least two things: (1) variation of λ values, and (2) variation of SSDs. This grouping approximately parallels the location-specific variation of λ values using the means of the demographically stochastic one-year transition matrix projections (Table 4-4).

In parsing the goodness-of-fit among individual's initial states, or size classes (S), we see that size classes 2-4 contribute to the lack of fit of the FS, SL model, whereas size class 1 does not. This suggests that transition counts from SC1 are similar among locations (Table 4-4C).

Projections of λ

We projected population abundance one year into the future, and also to the years 2030 and 2100. Means and confidence intervals of 10,000 simulations are provided so that the degree of demographic uncertainty in each estimate can be gauged. At each of these target years, we calculated future population abundance, and from that metric we calculated λ and percent cover. Lambda values projected one year into the future reflect the current momentum of population growth most accurately, whereas λ values at target years in the future reflect longer-term dynamics. Only Jamaica and Navassa exhibit positive rates of change in population size over the long term. Importantly, rates for Florida and Puerto Rico bracket 1 (population stasis) in the one-year projection. However, by 2030, neither confidence interval includes 1, and a decrease in population size is predicted. Population growth for these locations is predicted to be negative over all projection horizons (Table 4-6).

Recent and projected percent cover

Recent

Over the course of the study, percent cover declined in three locations (CUR, FL, and PR) and increased in three locations (JAM, NAV, and VG), although only the trend in Curaçao is significant. Relative to each location's initial percent cover, decreases were slightly greater than increases (-38, -35, and -13% versus, 9, 33, and 8 %, respectively). All three locations that experienced decreases in percent cover suffered significant storm damage over the course of the study.

Examining rates of recovery before and after storms reveals an interesting distinction. In Florida, severe hurricanes directly affected the study area during the first two years of surveying (2004 and 2005). During this time period, cover decreased by 51% (from 6.3% in 2004 to 3.1% in 2006). In the subsequent five years of relatively calm conditions, cover increased by 33% (to 4.1%). Similarly, in Curaçao a 2008 hurricane caused a 54% decrease in cover (from 7.7% in 2008 to 3.6% in 2009). In the subsequent two years, cover increased by 22%, a recovery rate 1.7 times that of Florida.

Projected

Projections of percent cover incorporate the dynamics captured in the mean matrices as well as the demographic stochasticity inherent in each location. In Puerto Rico, a strong downward trend in percent cover over the course of the study is predicted to continue to zero (Figure 4-6, Table 4-A5). In Curaçao and Florida, despite increases in percent cover after storms, cover is predicted to fall below 2% by 2030 before disappearing completely by 2100. In Navassa, cover increased by 33% over the study period, but percent cover asymptotes at 9% due to a λ of exactly 1 (λ in 2100 = 1.005, CI 1.003, 1.006). In contrast, percent cover in Jamaica was nearly stable over the study period but is predicted to rise steeply, reaching 5.43% (95% CI: 3.64-7.43) by 2030 and 21.14% (95% CI: 10.82-33.85%) by 2100. These increases are due to a 2% per year rate of increase in population abundance (mean λ = 1.02, 95% CI: 1.013-1.026).

Translating units from number of individuals (abundance) to percent cover is essential for a precise portrayal of *Acropora palmata* dynamics. In all locations that exhibited an increase in percent cover (JAM, NAV, and VG), a decrease in abundance was concomitant. This apparent paradox makes sense considering the relatively high rate of mortality for the smaller size classes even during calm years. If colonies grow from one size class to another while small individuals die, percent cover increases while abundance decreases. The reverse is also true. In Curaçao, a decrease in percent cover was accompanied by a 51% increase in abundance. In this case, storms caused breakage, increasing the number of colonies by fragmentation. Since percent cover relates to reef accretion and habitat complexity, it is a more appropriate response variable than abundance.

DISCUSSION

General trends

Acropora palmata population dynamics reveal important patterns of change in abundance and cover that cannot be realized by straightforward trend analysis of these variables over time. Understanding the variability in population growth rates on temporal and spatial scales is critical to assessing the vulnerability of populations threatened with extinction. Using data collected from 2004 to 2011 in three primary and three secondary locations across the Caribbean Sea, we estimated these rates of change in population size and the variability therein. Assuming *A. palmata* is structured in four size classes, and using matrix population modeling, we estimated and analyzed more detailed life history parameters as well, including fragmentation, a key aspect in *A. palmata* dynamics. We discovered important variations and similarities across space and time, explored the role of hurricanes as a structuring force in *A. palmata* population dynamics, and hypothesized about the dynamics associated with *A. palmata* resilience.

Although rates of change in abundance and percent cover during the study period were equivocal, the underlying dynamics are not. The general trend for *A. palmata* is further reductions in population size and extent by 2030 if background environmental conditions remain unchanged. These results are corroborated by analyses of annual growth rates, by percent cover projections, and by examining the matrices themselves. The following discussion focuses mainly on results from the three primary study locations, Curaçao, Florida, and Jamaica, where surveys were replicated over several years and patterns can be assessed with greater confidence.

Common response to a temporal event – storms

We witnessed a common effect of storms on adult mortality, population size structure and growth rate. In Chapter 2 we showed an example of storm dynamics in Florida. Here we parameterized storm dynamics in two additional locations, Puerto Rico and Curaçao. In all locations, during storm years the largest adults (SC4) have a higher probability of whole-colony mortality as well as an increased probability of shrinking. Also, relative abundance of large individuals decreases with respect to that of small individuals. This is because large colonies fragment and become smaller, and those fragments stay on the reef. Over this time scale we can also witness the converse: In areas without storms, the relative abundance shifts from small size classes to larger size classes as colonies grow. Where there were enough data after a storm, we witnessed potential recovery (as in the growth from smaller to larger size classes in Curaçao) or lack thereof (as in Florida) (Figure 4-2). Population growth rate was below 1 during storm intervals regardless of location. It may seem obvious that population growth rate decreases during a storm, but considering fragmentation, this was not a foregone conclusion (see Discussion of Lirman 2003 below).

Though reduction in population abundance due to storms was measured, the less-than-decadal time scale of this study is insufficient to capture recovery of a population from a major hurricane. In Florida, two Category 3 or greater hurricanes pummeled the survey area in 2005. The frequency of such an event in a 250 nm radius from the study site was once every 20 years since 1851 (Table 4-7). Thus recovery would not be expected in less than 20 years at this location. In the five other locations studied, the frequency of this same event was far less, having never occurred in Curaçao in 150 years of record-keeping. A recovery interval of approximately 20 to 50 years is also seen on Hawaiian reefs recovering from lava flows (Grigg and Maragos 1974).

Our results are less optimistic than those obtained by Lirman (2003), who found that medium-intensity storms every five years result in an increase in the abundance of colonies. The reason for this distinction is important. In the present study, every transition rate was parameterized during storm and non-storm years. In Lirman's study, fragmentation rates were parameterized explicitly during storms of varying intensity. Growth rates, however, were parameterized solely during calm years and assumed to remain constant. In our parameterization, we found that growth present during calm years ceases almost entirely during storm years (Table 4-A1 and 4-A2). Thus, this assumption appears erroneous at worst or overly optimistic at best.

Spatial variation

Due to the hierarchical survey design across space and a three-year period (2007-2010) during which five of the locations were surveyed, we were able to discern spatial variability in transition counts, including mortality. Using log-linear analysis on the surveyed *Acropora palmata* populations of Curaçao, Florida, Jamaica, Navassa, and Puerto Rico, we discovered that variation in transition is homogenous across distances less than 30 km and non-homogenous across distances greater than 250 km.

There is weaker evidence that variation remains homogenous at all distances less than 190 km ($p < 0.10$). This result suggests that five locations that span the Caribbean Sea have characteristically different *A. palmata* population dynamics.

This is an important discovery, from both a biological and conservation point of view. *Acropora palmata* is ecologically constrained, growing only in shallow waters, requiring relatively heavy wave action for sediment sloughing (Adey 1978, Geister 1977, Rogers 1983), and relying primarily on fragmentation for population expansion. Yet demographic rates of size class 1 (0-10 cm) were similar among locations, and no clear pattern emerged for location-specific fragmentation rates. This suggests that the location-specific differences are a result of varying environmental conditions that affect adult rates of growth and recovery.

Pairwise comparisons of locations confirmed that the results of the spatial analysis were not confounded by the effects of storms, which affected two of the locations (Curaçao and Puerto Rico). Under this analysis, if storms dictated the dynamics above and beyond inherent differences in location, Curaçao and Puerto Rico would have grouped together, but this was not the case. Further, analyzing mean matrices across all years versus mean matrices with storm years removed had different effects in Curaçao and Florida. In Florida, rate of change in population size, λ, flipped to > 1, whereas in Curaçao it did not. (Table 4-A1 and 4-A2). A simple examination of the annual matrices for each location reveals that λs for calm years in each site are characteristically different between the two locations.

Potential explanations of spatial differences

High sea urchin density

The most striking difference we quantified was between Jamaica, where populations is projected to grow in abundance, and all other locations, where population is projected to remain stable or decline. Further, Jamaica is the only location where both abundance (from the originally surveyed five plots) and percent cover increased over time. Our motivation for including Jamaica in the *A. palmata* demographic monitoring surveys was due to the remarkable recovery of the sea urchin *Diadema antillarum* at this location. Like all herbivores, this urchin grazes the reef substrate, consuming turf algae and clearing the substrate for the settlement of crustose coralline algae as well as coral sexual recruits (Edmunds and Carpenter 2001). But unlike other herbivores, *D. antillarum* has played the role of an entire guild, as it was the only abundant herbivore maintaining the dominance of corals on the overfished reefs of Jamaica before the 1980s (Hughes 1984, Jackson 1997).

To quantify the density of *Diadema antillarum*, we counted urchins in two 10 m x 1 m belt transects directly through the *A. palmata* demographic monitoring plots. These surveys were conducted in 2007 in four of the six study locations: Curacao, Florida, Jamaica, and Virgin Gorda. Surveys were repeated annually in Jamaica. Density of urchins was nearly an order of magnitude greater in Jamaica than in any other location (Table 4-7), suggesting that positive rates of growth in the Jamaican *A. palmata* population may be facilitated by high urchin density. This gives hope that

Jamaican reefs were not destroyed beyond repair, and it confirms the importance of including Jamaica in this study.

Historical extent and current availability of substrate

Acropora palmata dominated the shallow reefs throughout the Caribbean for half a million years, virtually unchanged until a few decades ago (Geister 1977, Adey 1978, Jackson 1992). From Jamaica we have both the fossil record and a detailed descriptions of *A. palmata*'s extent from the 1950s, before any populations collapsed (Goreau 1959). The ecological description provides us with data on the extent and density of *A. palmata* that those reefs are capable of hosting (e.g. quantitative transects in Pandolfi and Jackson 2001). Expectations of extent and density will differ, however, in different locations. Consistently high wave energy, for example, limits *A. palmata* abundance to solitary individuals in the exposed shorelines of the lesser Antilles and the exposed eastern shores of the Bahamas (Pandolfi and Jackson 2001), whereas areas of intermediate energy allow *A. palmata* to form luxuriant thickets in parts of Puerto Rico and patchily in the Florida Keys and Curaçao (van Duyl 1985, *Acropora* Biological Review Team 2005). Thus in the three primary locations, a recovery goal of "patchy thickets" at the very least, and thickets at best (e.g. in Jamaica), would be reasonable.

Potential loss of resilience in Florida

Only with a reasonable depiction of how *Acropora palmata* dynamics vary across space can we start to design location-specific management criteria. Although the goals may be common across locations (increase abundance and extent of *A.*

palmata), the techniques to achieve these goals and the expected outcomes will be different. In Florida, storms recur frequently, and population growth rates (λs) are > 1 in calm years, meaning fragmentation and attachment are occurring on an ongoing basis. Meanwhile, the relative abundance of large individuals has not increased in the six years since the most recent severe storm, meaning that fragmentation of the largest individuals is greater than or equal to growth from smaller size classes. This is likely due to excess nutrients in Florida (compared with Jamaica, for example) (La Pointe 1997). The lack of growth to larger size classes could signify that Florida's population is below some resilience threshold.

In contrast, relative abundance of the larger size classes increased in the two years after the storm in Curaçao (Figure 4-2). Thus, the slow and steady growth with minimal fragmentation that we originally expected to witness in this population could be occurring. Predicted percent cover in this case would be overly pessimistic, as it assumes that a severe hurricane (as experienced in 2008) would occur every six years. We know from hurricane tracks that this frequency is far lower. (Future simulations will account for reduced frequency, and may incorporate matrices typifying other extreme events such as bleaching or disease outbreaks.) Despite rates of population depletion rather than expansion and a significant decrease in percent cover over the survey interval, Curaçao still has the potential to exhibit natural resilience.

Resilience is a system's capacity to absorb disturbance while retaining the self-organizing capabilities to maintain its essential structure, function, and feedbacks (Walker 2009, Hughes et al. 2010). We have highlighted a potential distinction between current levels of resilience in Florida and Curaçao. There is a spectrum in corals, from fast-growing, easily-fragmented species that reside in the shallows to slow-growing, more massive species that dwell in deeper reef zones. *Acropora palmata* defines the extreme, as it resides in the shallowest reef environment and relies primarily on fragmentation for population expansion. Could a similar resilience gradient exist within the species? Could populations that are frequently subjected to severe storms (as in Florida) grow faster or fragment more easily than populations that rarely experience severe storms (as in Curaçao)? We present annual *A. palmata* population matrices for Curaçao and Florida in Tables 4-A1 and 4A-2, respectively. During five non-storm years in Florida, population growth rate, λ, exceeds 1 in four of the five years. During non-storm years in Curaçao, $\lambda > 1$ in just one of four years. Could the Florida population be better adapted to fragment and regrow in response to storms than Curaçao's population? If so, this might explain why our original expectation that Curaçao would exhibit stable rates of population growth was not met: because an uncharacteristic storm occurred.

Given that Florida *A. palmata* populations are adapted to fragmentation in high-energy environments, they often have a high proportion of damaged or exposed tissue that is subject to stress. They evolved "betting" on a future in which exposed tissue could heal quickly, but faced with increased sediments, sewage, algae, bacteria, disease, and acidity, that is no longer the case. This newfound lack of resilience may explain why Florida's *A. palmata* population is more susceptible to population decline than other populations. The only known genetic differentiation among populations that could be associated with this phenomenon is the low genotypic diversity in Florida relative to Curaçao (Williams et al. 2010). Florida's low genotypic diversity, however, is likely a result of the phenomenon (of frequent fragmentation), rather than a specialized genetic adaptation.

The resilience of *A. palmata* can also be gauged by the 30-year path of recovery in Jamaica. Severe storms are expected to affect the north coast of Jamaica only rarely; thus, it is possible that we are witnessing the early stages of recovery. What remains to be seen is if recovery can proceed to a state such that the vast thickets of "the *palmata* zone" return.

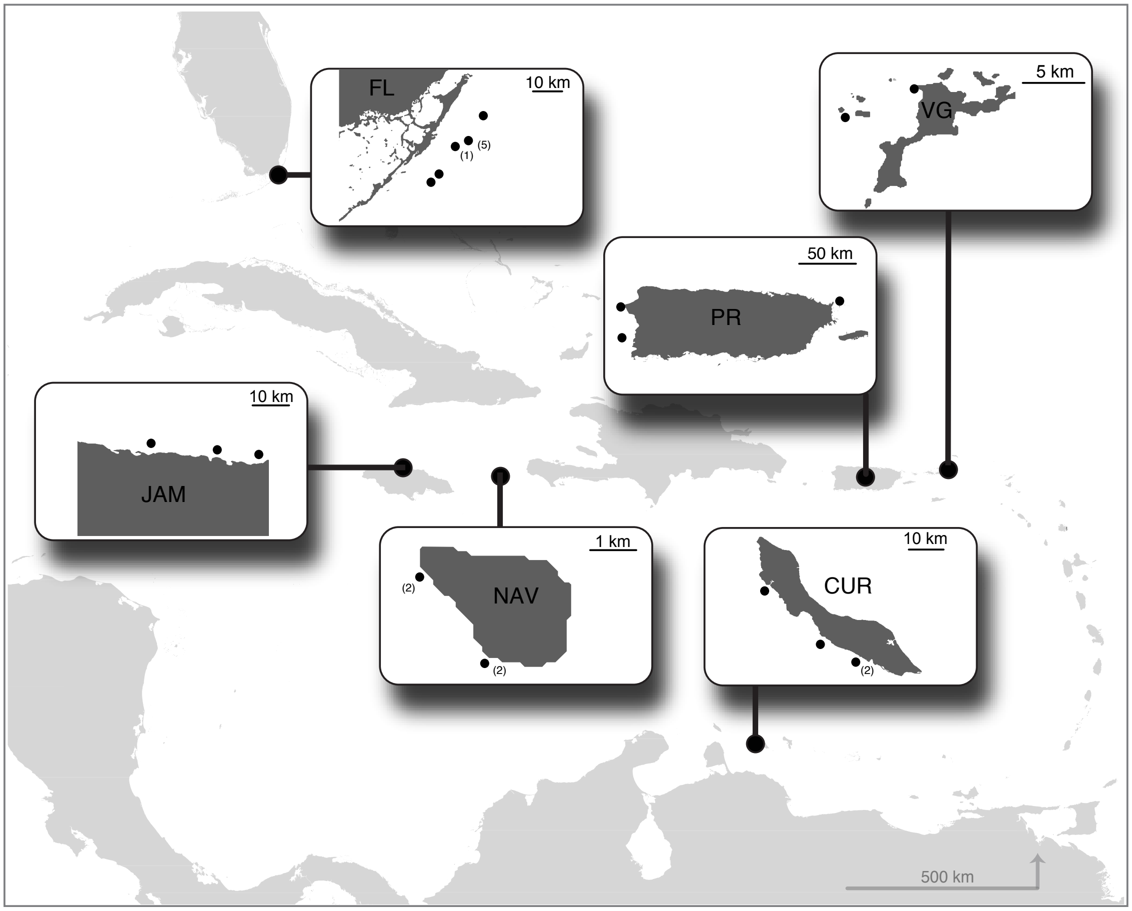

Figure 4-1: Map of the Caribbean Sea with inset maps of *Acropora palmata* demographic survey locations in Florida (FL), Puerto Rico (PR), Virgin Gorda, British Virgin Islands (VG), Curaçao (CUR), Navassa (NAV), and Jamaica (JAM). Circles represent survey sites with three replicate plots per site, except where numbers indicate a different number of plots.

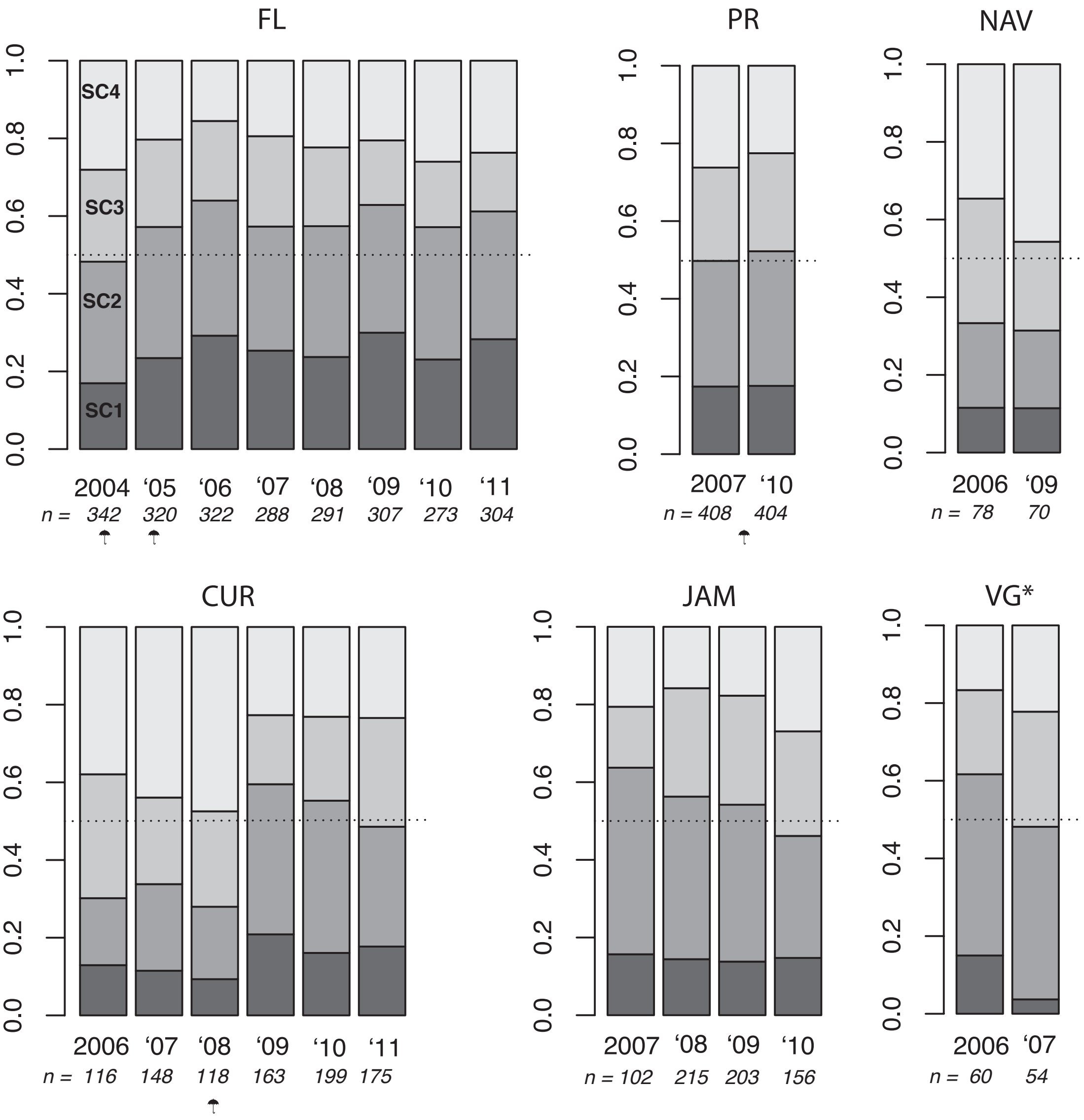

Figure 4-2: Relative abundance per size class per survey for each location. Size classes (SC) 1-4 have average planar dimension of 7, 20, 45, and 100 cm, respectively. In Florida (FL) abundance is based on 15 plots. Nine plots were surveyed in Puerto Rico (PR). Four plots were surveyed in Navasa (NAV). In Curacao (CUR), abundance is calculated from seven plots in 2006 and 2009, and eight plots all other years. In Jamaica (JAM), five plots were surveyed in 2007 and nine plots in 2008-2010. Six plots were surveyed in Virgin Gorda (VG). *In VG new fragments were not tallied, and thus SC1 is underrepresented in 2007. ☂ Umbrella represents years during which significant storm damage occurred.

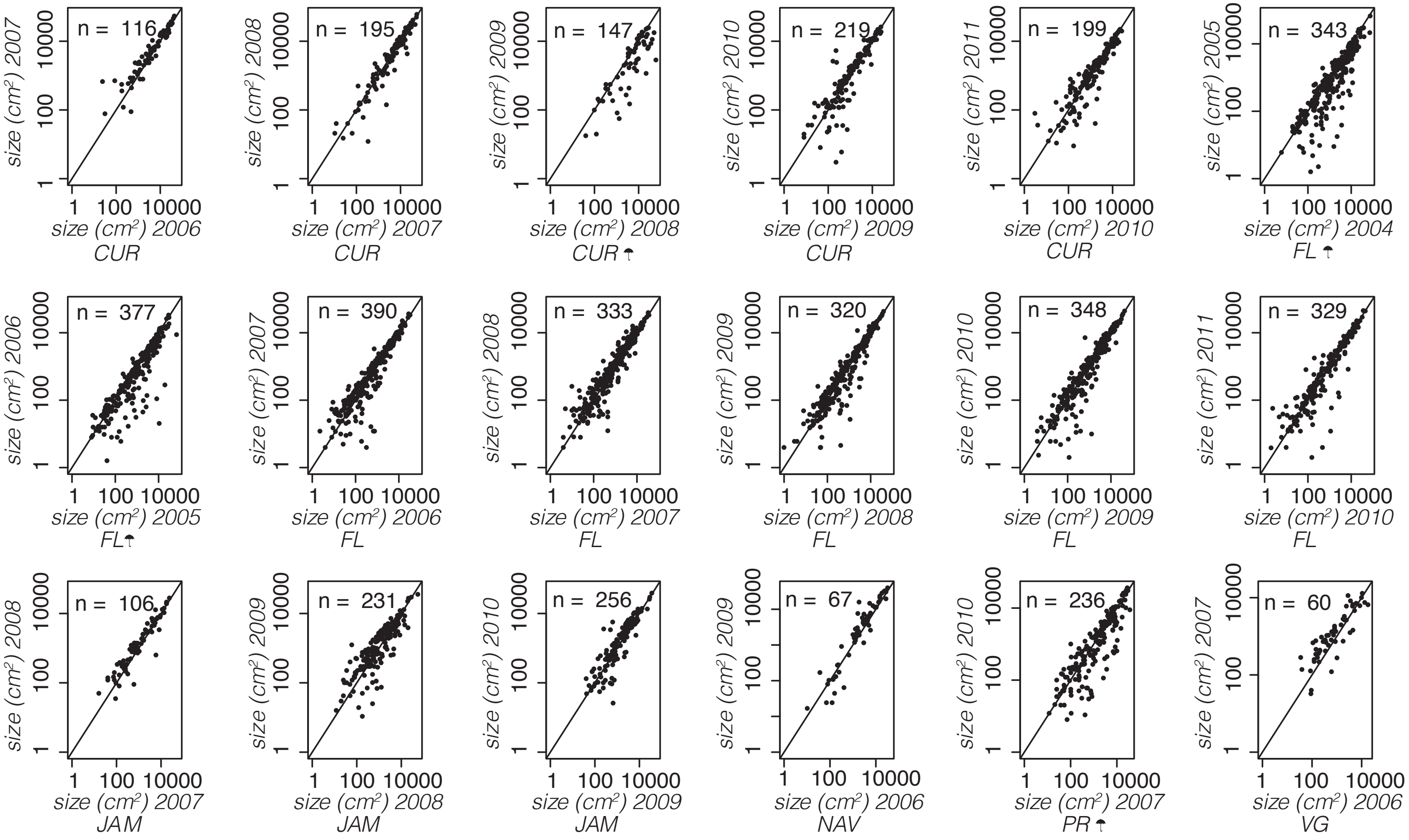

Figure 4-3: Size in cm^2 of individual *Acropora palmata* colonies as measured during the initial survey and each subsequent survey in Curaçao (CUR), Florida (FL), Jamaica (JAM), Navassa (NAV), Puerto Rico (PR), and Virgin Gorda (VG). Mortality (reduction in size to 0) is not presented here, as size is presented on a log scale. Annual mortality rates are included in annual matrices in Appendices 4A-1, 2, and 3. *n* represents the number of colonies during the earlier of the two years in each plot. ☂ Umbrella represents a time interval during which significant storm damage occurred.

Table 4-1: Triennial matrix population models. The full model, $\mathbf{A_3}$, is split into component matrices, $\mathbf{T_3}$, the transition matrix, and $\mathbf{F_3}$, the fertility matrix. Surveys were conducted in 2007 and 2010. See Appendix for more precise data collection times. Departures from a three-year survey interval are as indicated. Matrices for Jamaica are based on the five plots established in 2007. For each location, rate of change in population size, λ_3, is shown for $\mathbf{T_3}$ and $\mathbf{A_3}$, and $\lambda_3^{(1/3)}$ values are approximately but not exactly equal to λ_1 values in Figure 4-4. Lambda values for Navassa are exactly equal to 1 because of the lack of transitioning into or out of size classes 3 and 4. See text for additional explanation.

		T_3								A_3				λ_{3T}	λ_{3A}
	SC	***1***	***2***	***3***	***4***		***3***	***4***		***1***	***2***	***3***	***4***		
Curaçao	***1***	0.06	0.03	0.00	0.00		0.06	0.43		0.06	0.03	0.06	0.43		
	2	0.06	0.18	0.21	0.02	+	0.13	0.90	=	0.06	0.18	0.34	0.92	0.441	0.812
	3	0.00	0.06	0.09	0.14		-	0.45		0.00	0.06	0.09	0.58		
	4	0.00	0.03	0.12	0.37		-	0.26		0.00	0.03	0.12	0.63		
	mort	0.88	0.70	0.58	0.48										
Florida	***1***	0.26	0.10	0.04	0.00		0.09	0.46		0.26	0.10	0.14	0.46		
	2	0.25	0.34	0.16	0.02	+	0.09	0.46	=	0.25	0.34	0.26	0.48	0.93	1.04
	3	0.01	0.12	0.36	0.09		-	0.09		0.01	0.12	0.36	0.18		
	4	0.00	0.02	0.30	0.88		-	0.00		0.00	0.02	0.3	0.88		
	mort	0.48	0.42	0.13	0.02										
Jamaica	***1***	0.06	0.00	0.07	0.00		0.10	0.45		0.06	0.00	0.16	0.45		
	2	0.13	0.17	0.07	0.00	+	0.20	0.95	=	0.13	0.17	0.27	0.95	0.788	1.069
	3	0.06	0.21	0.20	0.21		-	0.11		0.06	0.21	0.20	0.32		
	4	0.00	0.11	0.40	0.63		-	0.00		0.00	0.11	0.40	0.63		
	mort	0.75	0.51	0.27	0.16										
Navassa	***1***	0.50	0.25	0.00	0.00		0.01	0.07		0.50	0.25	0.01	0.07		
2.5 y	***2***	0.33	0.58	0.00	0.00	+	0.03	0.17	=	0.33	0.58	0.03	0.17	1*	1*
	3	0.00	0.00	0.63	0.08		-	0.00		0.00	0.00	0.63	0.08		
	4	0.00	0.00	0.38	0.92		-	0.00		0.00	0.00	0.38	0.92		
		0.17	0.17	0.00	0.00										
Puerto Rico	***1***	0.17	0.08	0.01	0.01		0.07	0.38		0.17	0.08	0.08	0.39		
2.75 y	***2***	0.21	0.31	0.12	0.07	+	0.09	0.51	=	0.21	0.31	0.21	0.59	0.624	0.910
	3	0.03	0.11	0.31	0.11		-	0.40		0.03	0.11	0.31	0.51		
	4	0.01	0.00	0.19	0.51		-	0.15		0.01	0.00	0.19	0.66		
	mort	0.58	0.50	0.37	0.30										

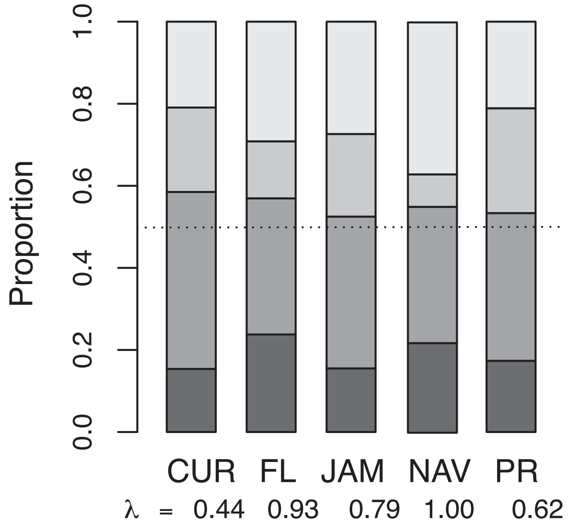

Figure 4-4: Stable size class distributions (SSDs) of *Acropora palmata* in Curaçao (CUR), Florida (FL), Jamaica (JAM), Navassa (NAV), and Puerto Rico (PR) as estimated from triennial matrices from 2007-2010. SSDs present the ultimate distribution of size classes (SCs) 1-4, for each location, assuming dynamics do not change. Lambda values from the **A** matrix are presented under the location names. The dotted line representing the 0.5 proportion is provided for visual clarity.

Table 4-2: Annual matrix population models, $\mathbf{A_1}$, split into component matrices, $\mathbf{T_1}$, transition matrix, and $\mathbf{F_1}$, fertility matrix. For locations with more than two surveys, Curaçao, Florida, and Jamaica, mean annual matrices are presented for ***n*** survey intervals. Mean matrices for all years without significant storm damage are presented for Florida (2004-2005 and 2005-2006 excluded) and Curaçao (2008-2009 excluded). * In Virgin Gorda, 1.75 years elapsed between surveys, and new fragments were not recorded. Mortality per size class, indicated below **T** for each location, is 1 minus the sum of the transitions for each size class. Annual rates of change in population size, λ_1, are presented for both **T** and **A** matrices. λ_1 values are converted to annual rates for Navassa and Puerto Rico, where survey intervals were 2.5 and 2.75 years respectively. Those matrices appear in Table 4-1.

			T_1					F_1			A_1				λ_{1T}	λ_{1A}
	n	***SC***	***1***	***2***	***3***	***4***		***3***	***4***		***1***	***2***	***3***	***4***		
Curacao	***5***	***1***	0.28	0.09	0.02	0.00	+	0.03	0.20	=	0.28	0.09	0.05	0.20	0.813	0.910
all years		***2***	0.13	0.48	0.10	0.00		0.06	0.35		0.13	0.48	0.16	0.35		
		3	0.00	0.11	0.60	0.08			0.11		0.00	0.11	0.60	0.19		
		4	0.00	0.00	0.10	0.77			0.03		0.00	0.00	0.10	0.80		
		mort	0.60	0.32	0.18	0.15										
Curacao	***4***	***1***	0.30	0.10	0.01	0.00	+	0.02	0.13	=	0.30	0.10	0.03	0.131	0.885	0.959
calm years		***2***	0.16	0.50	0.09	0.00		0.04	0.26		0.16	0.50	0.13	0.257		
		3	0.00	0.13	0.70	0.07			0.08		0.00	0.13	0.70	0.144		
		4	0.00	0.00	0.10	0.84			0.01		0.00	0.00	0.10	0.852		
		mort	0.54	0.27	0.11	0.09										
Florida	***7***	***1***	0.60	0.12	0.02	0.00	+	0.05	0.26	=	0.60	0.12	0.07	0.26	0.914	0.961
all years		***2***	0.12	0.60	0.17	0.01		0.04	0.22		0.12	0.60	0.21	0.23		
		3	0.00	0.08	0.62	0.11			0.05		0.00	0.08	0.62	0.16		
		4	0.00	0.00	0.12	0.86			0.00		0.00	0.00	0.12	0.86		
		mort	0.27	0.20	0.07	0.01										
Florida	***5***	***1***	0.58	0.12	0.02	0.00	+	0.05	0.25	=	0.58	0.12	0.07	0.25	0.965	1.018
calm years		***2***	0.16	0.62	0.14	0.00		0.04	0.19		0.16	0.62	0.18	0.20		
		3	0.00	0.09	0.64	0.07			0.05		0.00	0.09	0.64	0.12		
		4	0.00	0.00	0.15	0.93			0.00		0.00	0.00	0.15	0.93		
		mort	0.25	0.17	0.05	0.00										
Jamaica	***3***	***1***	0.21	0.07	0.01	0.00	+	0.06	0.30	=	0.21	0.07	0.07	0.30	0.906	1.020
all years		***2***	0.28	0.47	0.09	0.03		0.09	0.45		0.28	0.47	0.18	0.48		
		3	0.01	0.17	0.63	0.10			0.05		0.01	0.17	0.63	0.15		
		4	0.00	0.00	0.16	0.83			0.01		0.00	0.00	0.16	0.84		
		mort	0.50	0.29	0.11	0.05										
Navassa	***1***														1.000	1.000
Puerto Rico	***1***														0.842	0.966
Virgin Gorda*	***1***	***1***	0.22	0.00	0.00	0.00	+			=					0.988	-
1.75 y		***2***	0.33	0.68	0.15	0.00										
		3	0.00	0.29	0.54	0.10										
		4	0.00	0.00	0.23	0.90										
		mort	0.44	0.04	0.08	0.00										

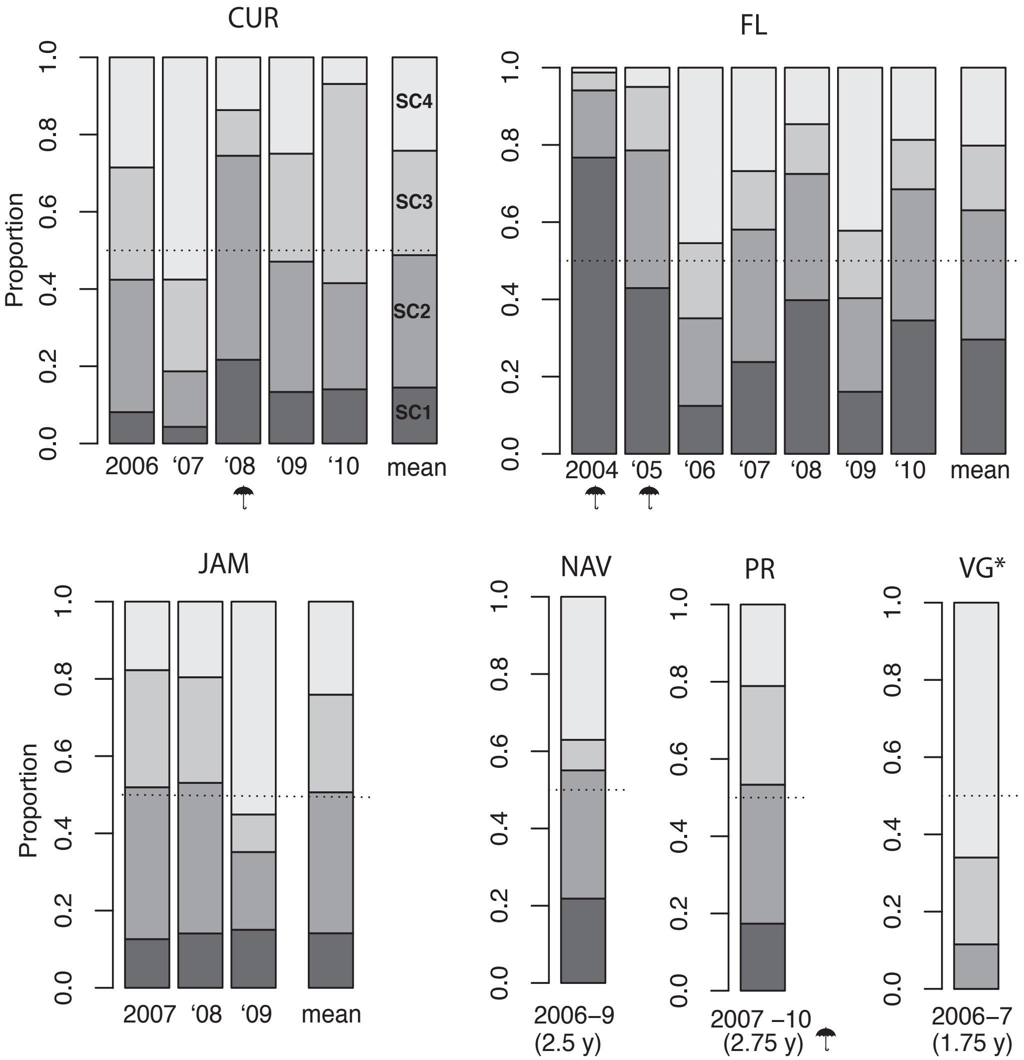

Figure 4-5: Stable size class distributions (SSDs) of *Acropora palmata* in Curaçao (CUR), Florida (FL), Jamaica (JAM), Navassa (NAV), Puerto Rico (PR), and Virgin Gorda (VG). SSDs present the ultimate distribution of size classes (SCs) 1-4, for each population, assuming dynamics do not change. The variability in results shows that dynamics are not stable among years, and that storm years have characteristically different dynamics. For locations with surveys repeated over several years (CUR, FL, and JAM), SSDs are based on approximately annual transition matrices with the initial survey year indicated on the x-axis. The SSD based on the mean matrix over all time intervals is also presented. For locations with only two surveys, the survey intervals are on the x-axis. ☂ Umbrella represents a time interval during which storm damage occurred. * Recruitment was not measured in Virgin Gorda (VG), thus the lower size classes are under-represented. The dotted line representing the 0.5 proportion is provided for visual clarity.

Table 4-3: Does site matter? A. Goodness of fit (G^2) values and corresponding degrees of freedom (*df*) and *p*-values are presented for a comparison of two log-linear models. The log-linear models parameterize transition counts from Curaçao (CUR), Florida (FL), Jamaica (JAM), Navassa (NAV), Puerto Rico (PR), and Virgin Gorda (VG). The saturated log-linear model, FSXT, comprises four factors: initial state (size class, *S*), resulting fate (growth, stasis, or shrinkage to a size class, or death, *F*), site (*X*), and time (number of transition matrices over the study, *T*). FSXT is compared to the log-linear model excluding all interactions of fate (*F*) and site (*X*), the FST, SX, XT model. G^2 for the fully saturated model is always 0. For each location, including site (X) as a factor does not improve the model significantly at the $p = 0.05$ level. We come closest to rejecting the null hypothesis that FSXL is a better model in Puerto Rico, where sites were located geographically further apart than those in other locations. B. Goodness-of-fit is parsed for each site.

A.

Location	*Number of sites*	G^2	*df*	*P*
CUR	3	90.602	160	1.000
FL	5	241.622	448	1.000
JAM	3	61.524	64	0.565
NAV	2	3.572	16	0.999
PR	3	42.526	32	0.101
VG	2	6.041	16	0.988

B.

Location	*Site*	G^2	*df*	*P*
CUR	BB	26.424	53	0.999
	SM	30.205	53	0.996
	SQ	33.973	53	0.982
FL	CF	86.187	90	0.582
	EL	20.418	90	1.000
	FR	59.202	90	0.995
	KL	20.418	90	1.000
	ML	55.396	90	0.998
JAM	PTB	18.689	21	1.000
	RB	25.232	21	1.000
	SR	17.603	21	1.000
NAV	LL	1.846	8	0.985
	NW	1.725	8	0.988
PR	CR	9.632	11	0.534
	LC	15.208	11	0.156
	TP	17.685	11	0.079
VG	MP	2.619	8	0.956
	WD	3.423	8	0.905

Table 4-4: Does location matter? Model performance. A. Goodness-of-fit (G^2) of fully saturated log-linear model including all interactions of fate (*F*), state (*S*), and location (*L*), the FSL model, is compared with the log-linear model excluding the effect of location on fate (FS, SL). Models were parameterized by 3-year transition counts in Curaçao, Florida, Jamaica, Navassa, and Puerto Rico. The FSL model explains the data significantly better than the model excluding location as a factor. B. G^2 parsed for each location reveals that all locations except Puerto Rico contribute to the lack of fit of the FS, SL model. Degrees of freedom for each row are 64/5. C. G^2 parsed for *S* reveals that size classes 2-4 contribute to the lack of fit of the FS, SL model, whereas size class 1 does not, suggesting that transition counts from size class one are similar among locations. Degrees of freedom for each row are 64/4.

A.

Model	***G^2***	***df***	***P***
FS, SL	177.78	64	**0.00**
FSL	0.00	0	

B.

Location	***G^2***	***P***
CUR	49.54	**0.00**
FL	40.04	**0.00**
JAM	23.65	**0.03**
NAV	49.70	**0.00**
PR	14.85	0.30
Sum	177.78	

C.

SC	***G^2***	***P***
1	17.71	0.34
2	37.75	**0.00**
3	56.06	**0.00**
4	66.26	**0.00**
Sum	177.78	

Table 4-5: Pairwise comparisons of saturated log-linear model with log-linear model excluding the effects of location as a factor influencing fate (FS, SL model). Transition counts over an approximate three-year time period are compared between the following locations: Curaçao (CUR), Florida (FL), Jamaica (JAM), and Navassa (NAV). Goodness-of-fit values are presented in the table above and corresponding p-values are presented in the table below. *p*-values < 0.05 are in bold.

G^2	***FL***	***JAM***	***NAV***	***PR***
CUR	**84.047**	**22.352**	**87.490**	**29.840**
FL	**-**	**28.967**	**21.130**	**46.277**
JAM	**-**	**-**	**40.726**	**29.145**
NAV	**-**	**-**	**-**	**53.192**

p-value	***FL***	***JAM***	***NAV***	***PR***
CUR	**0.000**	0.132	**0.000**	**0.019**
FL	**-**	**0.024**	0.174	**0.000**
JAM	**-**	**-**	**0.001**	**0.023**
NAV	**-**	**-**	**-**	**0.000**

Table 4-6: Table of λ values. Rate of change in population size is estimated for locations excluding (λ_T) and including (λ_A) recruitment. Besides the deterministic values, all λs incorporate demographic stochasticity by assuming each column of **T,** the transition matrix, is a multinomial probability distribution, and the fertility rates in **F,** the fertility matrix, are assumed to come from a Poisson distribution. For locations with more than two surveys, Curacao (CUR), Florida (FL), and Jamaica (JAM), λ is evaluated on the mean matrix over all transitions in that location (*n* = number of transitions). (See Appendix for annual matrices.) Stochastic estimates are based on 10,000 simulations, and 95% confidence intervals are shown. Lambda is evaluated over one year, and in the years 2030 and 2011. * Recruitment was not measured in Virgin Gorda, thus λ_A could not be evaluated.

		Deterministic	**One Time Step**			**2030**			**2100**			**Deterministic**	**One Time Step**			**2030**			**2100**		
Location	***n***	λ_T	λ_T	**lci**	**uci**	λ_T	**lci**	**uci**	λ_T	**lci**	**uci**	λ_A	λ_A	**lci**	**uci**	λ_A	**lci**	**uci**	λ_A	**lci**	**uci**
FL	7	0.914	0.844	0.806	0.882	0.889	0.873	0.902	0.911	0.876	0.938	0.961	0.983	0.928	1.039	0.965	0.949	0.979	0.957	0.929	0.975
CUR	5	0.813	0.710	0.646	0.771	0.786	0.724	0.829	0.807	0.724	0.879	0.910	0.896	0.806	0.989	0.905	0.860	0.939	0.895	0.837	0.940
JAM	3	0.906	0.792	0.731	0.853	0.887	0.862	0.907	0.905	0.865	0.942	1.020	1.051	0.949	1.154	1.022	1.003	1.038	1.020	1.013	1.026
PR	1	0.842	0.814	0.788	0.837	0.830	0.804	0.853	0.845	0.800	0.897	0.966	0.975	0.946	1.003	0.967	0.950	0.983	0.962	0.932	0.978
NAV	1	1.000	0.979	0.959	0.994	0.987	0.984	0.990	0.996	0.996	0.996	1.000	1.026	0.989	1.064	1.017	1.009	1.024	1.005	1.003	1.006
VG*	1	0.988	0.953	0.912	0.989	0.975	0.972	0.980	0.986	0.981	0.990	-	-	-	-	-	-	-	-	-	-

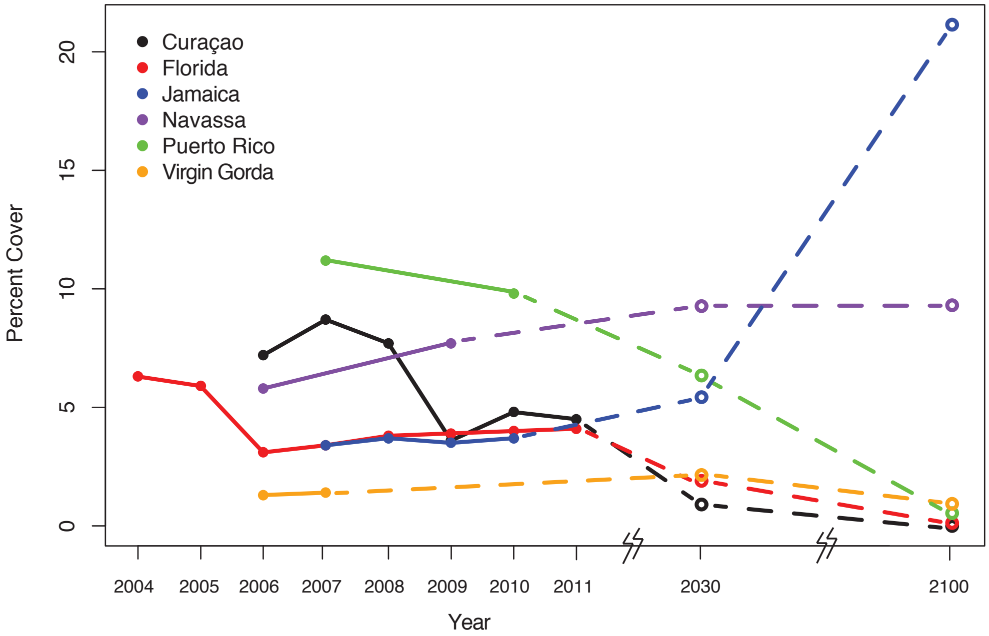

Figure 4-6: Percent cover of *Acropora palmata*. Solid circles represent data as measured and open circles represent projections. 95% confidence intervals are presented in Table 4-A5.

Table 4-7: Important ecological factors at each location. Surveys to measure *Diadema antillarum* density were conducted in 2007. Hurricane recurrence rates were calculated from within a 200 nm radius of the middle study site at each location using the Historical Hurricane Tracks tool (NOAA 2011).

Location	**Mean # of *D. antillarum*/m^2 (±SE)**	**Source**	**Annual probability of recurrence of >1 H3+**	**Genotypic diversity (Ng/N) mean ± SD**	**Source**
Curaçao	0.03 ± 0.03	Vardi unpubl.	0	0.67 ± 0.26	Williams et al. 2010
Florida	0.00 ± 0.00	Vardi unpubl.	0.05	0.22 ± 0.11	Williams et al. 2010
Jamaica	3.51 ± 0.59	Vardi unpubl.	0.02	-	-
Navassa	0.16 ± 0.02	Miller et al. 2008	0.01	1	Baums et al. 2006
Puerto Rico	0.00 ± 0.00	Ruiz-Ramos et al. 2011 (0 for 3 sites close to our study sites. 0 to 0.9 island wide)	0.01	0.77 ± 0.22	Baums et al. 2005
Virgin Gorda	0.53 ± 0.33	Vardi unpubl.	0.01	-	-

Table 4-A1: Matrix population models, **A,** split into component matrices, **T,** transition matrix, and **F,** fertility matrix for Curaçao. Each matrix represents an approximately annual transition. Surveys were conducted each spring except for 2009 when the survey was conducted in the summer, resulting in a slightly longer time interval in 2008-2009 and a slightly shorter interval for 2009-2010, as indicated. Rate of change in population size, λ, is shown for **T** and **A** of each time interval, and when the interval is different from 1, taken to root of the interval (Caswell 2001).

Curaçao

		T					***F***					***A***				λ_T	λ_A
	SC	***1***	***2***	***3***	***4***		***1***	***2***	***3***	***4***		***1***	***2***	***3***	***4***		
2006-7	***1***	0.27	0.05	0.00	0.00		-	-	0.02	0.16		0.27	0.05	0.02	0.16		
	2	0.27	0.65	0.08	0.00	+	-	-	0.05	0.37	=	0.27	0.65	0.13	0.37	0.95	1.13
	3	0.00	0.20	0.65	0.07		-	-	-	0.18		0.00	0.20	0.65	0.25		
	4	0.00	0.00	0.22	0.89		-	-	-	0.02		0.00	0.00	0.22	0.91		
	mort	0.47	0.10	0.05	0.05												
2007-8	***1***	0.35	0.09	0.00	0.00		-	-	0.00	0.01		0.35	0.09	0.00	0.01		
	2	0.00	0.45	0.06	0.00	+	-	-	0.01	0.07	=	0.00	0.45	0.07	0.07	0.85	0.86
	3	0.00	0.12	0.64	0.05		-	-	-	0.02		0.00	0.12	0.64	0.06		
	4	0.00	0.00	0.03	0.85		-	-	-	0.00		0.00	0.00	0.03	0.85		
	mort	0.65	0.33	0.27	0.11												
2008-9	***1***	0.18	0.05	0.07	0.00		-	-	0.07	0.46		0.18	0.05	0.14	0.46		
1.25 y	***2***	0.00	0.41	0.17	0.00	+	-	-	0.11	0.73	=	0.00	0.41	0.28	0.73	0.59	0.72
	3	0.00	0.00	0.21	0.14		-	-	-	0.25		0.00	0.00	0.21	0.39		
	4	0.00	0.00	0.10	0.46		-	-	-	0.11		0.00	0.00	0.10	0.57		
	mort	0.82	0.55	0.45	0.39												
2009-10	***1***	0.26	0.13	0.00	0.00		-	-	0.03	0.16		0.26	0.13	0.03	0.16		
0.75 y	***2***	0.24	0.49	0.07	0.00	+	-	-	0.07	0.35	=	0.24	0.49	0.14	0.35	0.81	0.95
	3	0.00	0.10	0.72	0.08		-	-	-	0.08		0.00	0.10	0.72	0.16		
	4	0.00	0.02	0.14	0.78		-	-	-	0.00		0.00	0.02	0.14	0.78		
	mort	0.50	0.27	0.07	0.14												
2010-11	***1***	0.31	0.13	0.02	0.00		-	-	0.04	0.18		0.31	0.13	0.06	0.18		
	2	0.13	0.40	0.14	0.00	+	-	-	0.05	0.24	=	0.13	0.40	0.18	0.24	0.85	0.87
	3	0.00	0.12	0.77	0.11		-	-	-	0.02		0.00	0.12	0.77	0.13		
	4	0.00	0.00	0.02	0.85		-	-	-	0.02		0.00	0.00	0.02	0.87		
	mort	0.56	0.36	0.05	0.04												

Table 4-A2: Annual transition and fertility matrices (**T** and **F**), and matrix population models, **A**, for *Acropora palmata* in the Florida Keys.

Florida		***T***					***F***					***A***				λ_T	λ_A
	SC	***1***	***2***	***3***	***4***		***1***	***2***	***3***	***4***		***1***	***2***	***3***	***4***		
2004-5	***1***	0.707	0.150	0.037	0.000	+			0.023	0.137	=	0.707	0.150	0.060	0.137	0.739	0.747
0.75 y	***2***	0.017	0.570	0.296	0.052				0.026	0.155		0.017	0.570	0.322	0.207		
	3	0.000	0.047	0.494	0.250					0.031		0.000	0.047	0.494	0.281		
	4	0.000	0.000	0.025	0.656					0.000		0.000	0.000	0.025	0.656		
	mort	0.276	0.234	0.148	0.042												
2005-6	***1***	0.600	0.130	0.042	0.015	+			0.075	0.394	=	0.600	0.130	0.117	0.409	0.759	0.800
0.75 y	***2***	0.053	0.546	0.194	0.031				0.080	0.419		0.053	0.546	0.274	0.450		
	3	0.000	0.046	0.625	0.185					0.062		0.000	0.046	0.625	0.246		
	4	0.000	0.000	0.014	0.723					0.031		0.000	0.000	0.014	0.754		
	mort	0.347	0.278	0.125	0.046												
2006-7	***1***	0.596	0.125	0.000	0.000	+			0.010	0.047	=	0.596	0.125	0.010	0.047	0.987	1.012
	2	0.128	0.589	0.091	0.000				0.026	0.126		0.128	0.589	0.117	0.126		
	3	0.000	0.125	0.773	0.040					0.000		0.000	0.125	0.773	0.040		
	4	0.000	0.000	0.121	0.960					0.000		0.000	0.000	0.121	0.960		
	mort	0.277	0.161	0.015	0.000												
2007-8	***1***	0.562	0.130	0.000	0.000	+			0.046	0.230	=	0.562	0.130	0.046	0.230	0.982	1.038
	2	0.247	0.652	0.090	0.000				0.040	0.202		0.247	0.652	0.130	0.202		
	3	0.000	0.065	0.701	0.071					0.036		0.000	0.065	0.701	0.107		
	4	0.000	0.000	0.194	0.929					0.000		0.000	0.000	0.194	0.929		
	mort	0.192	0.152	0.015	0.000												
2008-09	***1***	0.681	0.122	0.017	0.000	+			0.087	0.413	=	0.681	0.122	0.104	0.413	0.929	0.967
	2	0.116	0.582	0.220	0.000				0.063	0.297		0.116	0.582	0.283	0.297		
	3	0.000	0.112	0.542	0.092					0.031		0.000	0.112	0.542	0.123		
	4	0.000	0.000	0.068	0.908					0.000		0.000	0.000	0.068	0.908		
	mort	0.203	0.184	0.153	0.000												
2000-10	***1***	0.435	0.119	0.020	0.000	+			0.027	0.137	=	0.435	0.119	0.047	0.137	0.97	1.024
	2	0.217	0.574	0.137	0.000				0.022	0.109		0.217	0.574	0.159	0.109		
	3	0.000	0.079	0.569	0.079					0.063		0.000	0.079	0.569	0.143		
	4	0.000	0.010	0.235	0.921					0.000		0.000	0.010	0.235	0.921		
	mort	0.348	0.218	0.039	0.000												
2010-11	***1***	0.651	0.086	0.043	0.000	+			0.083	0.439	=	0.651	0.086	0.127	0.439	0.95	1.020
	2	0.095	0.710	0.152	0.014				0.045	0.238		0.095	0.710	0.197	0.252		
	3	0.000	0.054	0.630	0.056					0.113		0.000	0.054	0.630	0.169		
	4	0.000	0.000	0.152	0.915					0.000		0.000	0.000	0.152	0.915		
	mort	0.254	0.151	0.022	0.014												

Table 4-A3: Matrix population models, **A**, split into component matrices, **T**, transition matrix, and **F,** fertility matrix for Jamaica. Each matrix represents an approximately annual transition. Surveys were conducted each fall from 2007-2010, except 2008 when the survey was conducted in the summer, resulting in a slightly shorter time interval in 2007-2008 and a slightly longer interval for 2008-2009, as indicated. Rate of change in population size, λ, is shown for **T** and **A** of each time interval, and when the interval is different from 1, taken to root of the interval (Caswell 2001).

Jamaica

		T					***F***					***A***				λ_T	λ_A
	SC	***1***	***2***	***3***	***4***		***1***	***2***	***3***	***4***		***1***	***2***	***3***	***4***		
2007-8	***1***	0.19	0.04	0.00	0.00		-	-	0.10	0.45		0.19	0.04	0.10	0.45	0.93	1.25
0.75 y	***2***	0.31	0.51	0.07	0.05	+	-	-	0.17	0.81	=	0.31	0.51	0.24	0.86		
	3	0.00	0.28	0.73	0.05		-	-	-	0.11		0.00	0.28	0.73	0.16		
	4	0.00	0.00	0.20	0.84		-	-	-	0.00		0.00	0.00	0.20	0.84		
	mort	0.50	0.17	0.00	0.05												
2008-9	***1***	0.26	0.07	0.02	0.00		-	-	0.05	0.29		0.26	0.07	0.07	0.29	0.91	0.98
1.25 y	***2***	0.35	0.49	0.12	0.03	+	-	-	0.08	0.43	=	0.35	0.49	0.19	0.46		
	3	0.03	0.12	0.60	0.21		-	-	-	0.06		0.03	0.12	0.60	0.26		
	4	0.00	0.00	0.13	0.76		-	-	-	0.03		0.00	0.00	0.13	0.79		
	mort	0.35	0.32	0.13	0.00												
2009-10	***1***	0.18	0.10	0.00	0.00		-	-	0.04	0.16		0.18	0.10	0.04	0.16	0.90	0.92
	2	0.18	0.40	0.09	0.00	+	-	-	0.03	0.12	=	0.18	0.40	0.12	0.12		
	3	0.00	0.10	0.56	0.03		-	-	-	0.00		0.00	0.10	0.56	0.03		
	4	0.00	0.01	0.16	0.89		-	-	-	0.00		0.00	0.01	0.16	0.89		
	mort	0.64	0.39	0.19	0.08												

Table 4-A4: GPS waypoint of each *Acropora palmata* demographic monitoring plot, except Split Rock, Jamaica, for which landmarks were used for SR2 and SR3.

Location	Site	Plot	Latitude	Longitude
CUR	Blue Baai	BB1	12.13511	-68.98682
CUR	Blue Baai	BB2	12.13527	-68.98710
CUR	Blue Baai	BB3	12.13520	-68.98738
CUR	Boca Santa Marta	SM1	12.26790	-69.12822
CUR	Boca Santa Marta	SM2	12.26790	-69.12822
CUR	Boca Santa Marta	SM3	12.26683	-69.12720
CUR	Sea Aquarium Reef	SQ1	12.08417	-68.89493
CUR	Sea Aquarium Reef	SQ2	12.08365	-68.89467
CUR	Sea Aquarium Reef	SQ3	12.08312	-68.89585
FL	Carysfort Reef	CF1	25.22194	-80.21055
FL	Carysfort Reef	CF2	25.22178	-80.21060
FL	Carysfort Reef	CF3	25.22290	-80.20956
FL	Elbow Reef	EL1	25.14259	-80.25835
FL	Elbow Reef	EL2	25.14290	-80.25822
FL	Elbow Reef	EL3	25.14394	-80.25780
FL	Elbow Reef	EL4	25.14508	-80.25734
FL	Elbow Reef	EL5	25.14518	-80.25740
FL	French Reef	FR1	25.03393	-80.34941
FL	Key Largo Dry Rocks	KL1	25.12360	-80.29736
FL	Key Largo Dry Rocks	KL2	25.12290	-80.29787
FL	Key Largo Dry Rocks	KL3	25.12255	-80.29826
FL	Molasses Reef	ML1	25.00958	-80.37481
FL	Molasses Reef	ML2	25.00912	-80.37473
FL	Molasses Reef	ML3	25.01015	-80.37328
JAM	Pear Tree Bottom	PT1	18.46293	-77.35728
JAM	Pear Tree Bottom	PT2	18.46293	-77.35812
JAM	Pear Tree Bottom	PT3	18.46308	-77.35707
JAM	Rio Bueno	RB1	18.47908	-77.46003
JAM	Rio Bueno	RB2	18.47953	-77.46037
JAM	Rio Bueno	RB3	18.47868	-77.45997
JAM	Split Rock	SR1	18.49522	-77.62732
NAV	LuLu Bay	LB1	18.39664	-75.01895
NAV	LuLu Bay	LB2	18.39638	-75.01883
NAV	Northwest Point	NW1	18.41385	-75.02987
NAV	Northwest Point	NW2	18.41394	-75.02963
NAV	Northwest Point	NW3	18.41368	-75.02923
PR	Cayo Ron	CR1	18.10192	-67.28577
PR	Cayo Ron	CR2	18.10158	-67.28577
PR	Cayo Ron	CR3	18.09687	-67.28633
PR	La Cordillera	LC1	18.37970	-65.58231
PR	La Cordillera	LC2	18.37543	-65.56730
PR	La Cordillera	LC3	18.35043	-65.56541
PR	Tres Palmas	TP1	18.35047	-67.26656
PR	Tres Palmas	TP2	18.35013	-67.26633
PR	Tres Palmas	TP3	18.34670	-67.26350
VG	Mountain Point	MP1	18.50232	-64.41592
VG	Mountain Point	MP2	18.50272	-64.41600
VG	Mountain Point	MP3	18.50337	-64.41600
VG	West Dog	WD1	18.48295	-64.47060
VG	West Dog	WD2	18.48292	-64.47045
VG	West Dog	WD3	18.48282	-64.46955

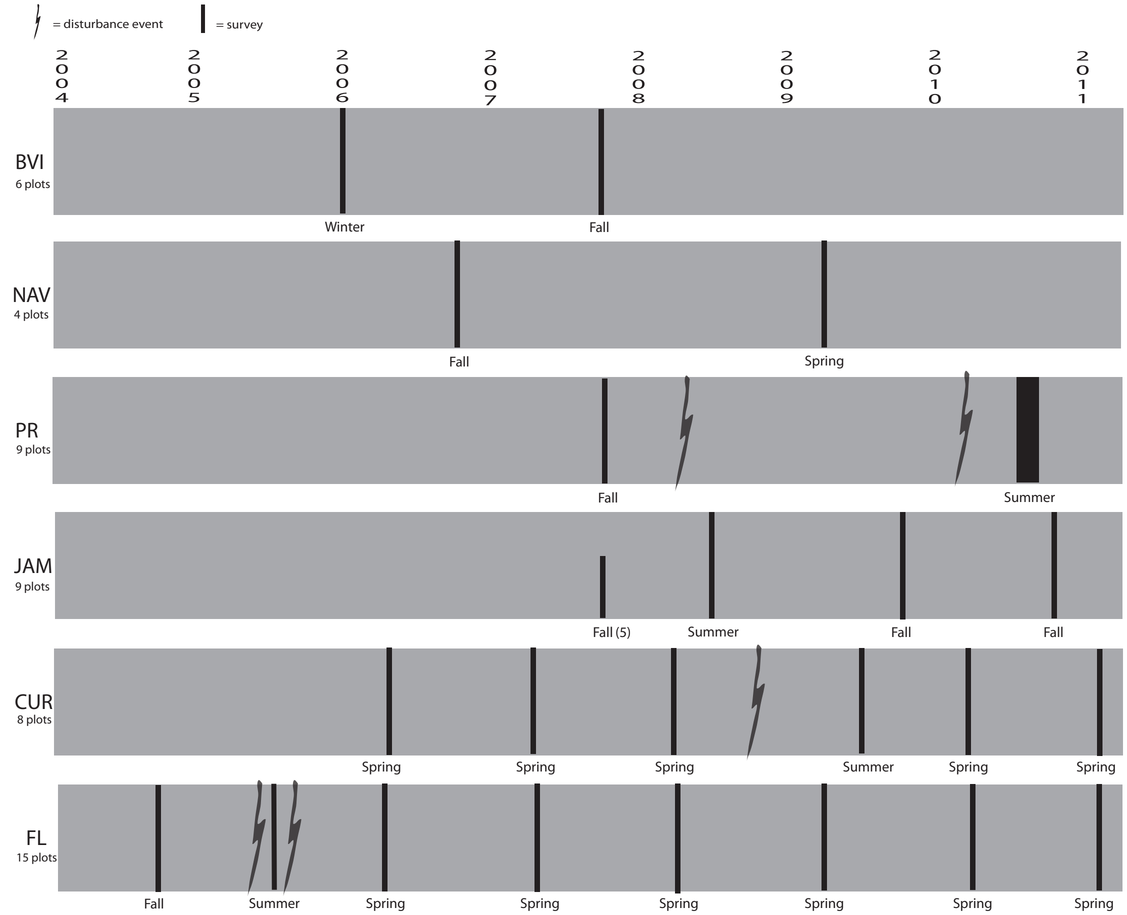

Figure 4-A1: Sampling schedule. The schedule for sampling at monitoring locations is shown along with the occurrence of disturbance events (indicated by lightning bolts).

Table 4-A5: Percent cover as projected in the years 2030 and 2100 based on 10,000 simulations of the mean **A** matrix incorporating demographic stochasticity. 95% confidence intervals are presented. * Projections in Virgin Gorda utilize the **T** matrix, as rates of fragmentation were not measured.

Location	*Area surveyed (m^2)*	*Mean % cover in 2030*	*lci*	*uci*	*Mean % cover in 2100*	*lci*	*uci*
Curaçao	1232	0.90	0.24	1.80	0.00	0.00	0.00
Florida	2309	1.90	1.26	2.61	0.12	0.00	0.40
Jamaica	1385	5.43	3.64	7.43	21.14	10.82	33.95
Navassa	616	9.27	8.30	10.13	9.31	8.33	10.16
Puerto Rico	1385	6.34	4.12	8.86	0.54	0.00	1.71
Virgin Gorda*	924	2.15	1.59	2.74	0.93	0.48	1.44

REFERENCES

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.

Adey W. 1978. Coral-Reef Morphogenesis - Multidimensional Model. Science 202:831–837.

Aronson, R., and W.F. Precht. 2001. White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460:25–38.

Baums, I. B., M. W. Miller, and M. E. Hellberg. 2005. Regionally isolated populations of an imperiled Caribbean coral, Acropora palmata. Molecular Ecology 14:1377–1390.

Baums, I. B., M. W. Miller, and M. E. Hellberg. 2006. Geographic variation in clonal structure in a reef-building Caribbean coral, Acropora palmata. Ecological Monographs 76:503–519.

Bries J. M., A. O. Debrot, D. L. Meyer. 2004. Damage to the leeward reefs of Curaçao and Bonaire, Netherlands Antilles from a rare storm event: Hurricane Lenny, November 1999. Coral Reefs 23:297–307.

Budd, A., and K. Johnson. 1999. Origination preceding extinction during late Cenozoic turnover of Caribbean reefs. Paleobiology 25:188–200.

Caswell H. 2001. Matrix population models. 2nd ed. Sunderland, MA: Sinauer Associates Inc.

Edmunds P., and R. Carpenter. 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proceedings of the National Academy of Sciences USA 98:5067–5071.

Gardner, T. A., I. M. Coté, J. A. Gill, A. Grant, and A. R. Watkinson. 2005. Hurricanes and Caribbean coral reefs: impacts, recovery, patterns, and role in long-term decline. Ecology 86:174–184.

Geister J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Proceedings, Third International Coral Reef Symposium 1: 23–29

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

Goreau T. 1959. The ecology of Jamaican coral reefs I. Species composition and zonation. Ecology 40:67–90.

Greenstein B.J., H.A. Curran, J.M. Pandolfi. 1998. Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean Province: a Pleistocene perspective. Coral Reefs 17:249–261.

Grigg R., and Maragos J. 1974. Recolonization of hermatypic corals on submerged lava flows in Hawaii. Ecology 55:387–395.

Hughes T. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. American Naturalist 123:778–795.

Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. Trends in Ecology & Evolution 25:633–642.

Jackson J.B.C. 1992. Pleistocene perspectives on coral-reef community structure. American Zoologist 32: 719–731.

Jackson J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, J.A. Estes, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637.

Jackson J.B.C, and T.P. Hughes. 1985. Adaptive strategies of coral-reef invertebrates. American Scientist 73:265–274.

Jackson, J. B. C. 1997. Reefs since Columbus. Coral Reefs 16:S23–S32.

Lapointe, B. E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography 42:1119–1131.

Lang J.C. 2003. Status of coral reefs in the western Atlantic: Results of initial surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) program. Atoll Research Bulletin 496:1–635.

Lessios H., D. Robertson, J. Cubit. 1984. Spread of *Diadema* mass mortality through the Caribbean. Science 226:335–337.

Lirman D. 1999. Reef fish communities associated with *Acropora palmata*: Relationships to benthic attributes. Bulletin of Marine Science 65:235–252.

McClenachan L. 2009. Documenting loss of large trophy fish from the Florida Keys with historical photographs. Conservation Biology 23:636–643.

Miller, M., A. Gleason, D. McClellan, G. Piniak, J. W. Wiener, A. Gude, and J. Schwagerl. 2008. The state of coral reef ecosystems of Navassa Island. Pages 117–130 in J. E. Waddell and A. M. Clarke, editors. The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2008. 569 pp., Silver Spring, MD.

Pandolfi, J. M., J. B. C. Jackson, N. Baron, R. H. Bradbury, H. M. Guzman, T. P. Hughes, C. V. Kappel, F. Micheli, J. C. Ogden, H. P. Possingham, and E. Sala. 2005. Ecology. Are U.S. coral reefs on the slippery slope to slime? Science 307:1725–1726.

Pandolfi J.M., and J.B.C. Jackson. 2006. Ecological persistence interrupted in Caribbean coral reefs. Ecology Letters 9:818–826.

Pandolfi J.M, and J.B.C. Jackson. 2001. Community structure of Pleistocene coral reefs of Curaçao, Netherlands Antilles. Ecological Monographs 71:49–67.

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

Ruiz-Ramos, D. V., E. A. Hernández-Delgado, and N. V. Schizas. 2011. Population status of the long-spined urchin *Diadema antillarum* in Puerto Rico 20 years after a mass mortality event. Bulletin of Marine Science 87:113–127.

van Duyl F. 1985. Atlas of the living reefs of Curaçao and Bonaire (Netherlands Antilles).

Walker B. 2009. Stockholm whiteboard seminar: the best explanation to resilience. www.youtube.com/watch?v= tXLMeL5nVQk&feature=related. Accessed online December 8, 2011.

Wapnick C.M., W.F. Precht, R.B. Aronson. 2004. Millennial-scale dynamics of staghorn coral in Discovery Bay, Jamaica. Ecology Letters 7:354–361.

Williams D.E., M.W. Miller, K.L. Kramer. 2006. Demographic monitoring protocols for threatened Caribbean *Acropora* spp. corals. NOAA Technical Memorandum NMFS-SEFSC-543. 91 pp.

Williams, D. E., A. J. Bright, K. L. Kramer, and M. W. Miller. 2010. Status of *Acropora palmata* in Curaçao: comparison with Florida Keys. NOAA Technical Memorandum. PRBD-11/01: 1-11.

Woodley J. 1992. The incidence of hurricanes on the north coast of Jamaica since 1870: are the classic reef descriptions atypical? Hydrobiologia 247:133–138.

Woodley J., E. Chornesky, P. Clifford, J. Jackson, L. Kaufman, N. Knowlton, J. Lang, M. Pearson, J. Porter, M. Rooney, et al. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science 214:749–755.

CHAPTER 5: Policy considerations for endangered corals

Corals are faring poorly throughout the world's oceans (Gardner et al. 2003, Bruno and Selig 2010). Due to its historically high human population density, combined with its relative paucity of coral species and much smaller regional expanse, corals in the Caribbean are faring worse than those in the Pacific (Carpenter et al. 2008). The distinction, however, is academic, as it represents a contest with no winners, only varying degrees of loss (Pandolfi et al. 2003, Newman et al. 2006). Whereas the decline of corals was previously a mystery, we now have a solid understanding of the drivers of decline, the consequences of coral decline for coral population dynamics, and the conservation actions that must be taken in order to prevent ecological extinction of remaining coral populations (Rohwer and Youle 2010). Here I summarize the threats that have driven corals to reach endangered species status, the recognition of one such species as endangered, the policy actions that must be taken in order to rescue it from near extinction, and the special considerations in endangered species management that must be considered because of the peculiar biology of corals.

Coral perils

For any coral population, three major anthropogenic pressures conspire to cause a decline in coral abundance or health: overfishing, eutrophication, and rising concentrations of carbon dioxide in the atmosphere and ocean. Overfishing causes a dearth of herbivores on coral reefs, which leads to uncontrolled algal growth (Jackson et al. 2001). These macroalgae compete with corals for space (McCook et al. 2001), shade corals from the sun, exude toxic secondary metabolites (Rasher and Hay 2010), harbor pathogens (Nugues et al. 2004), and exude excess photosynthate into the water column (Haas et al. 2010), processes that disrupt a coral's physiology (Barott et al. 2009), symbiotic relationships, and normal microbial community functioning (Kline et al. 2006, Smith et al. 2006).

Eutrophication in oligotrophic coral reef waters, stemming from excessive agricultural application and improperly treated human and animal sewage (Fabricius 2005), threatens corals by giving algae an additional competitive advantage (Burkepile and Hay 2009), reducing recruitment success of juveniles (Koop et al. 2001), driving seawater microbial communities away from their pristine states (Klaus et al. 2007, Garren et al. 2008), and spreading coral pathogens (Sutherland et al. 2010). Coral disease and rapid tissue mortality are common on algae-covered reefs.

Finally, burning fossil fuels (combined with removing carbon-sequestering forests) increases the concentration of carbon dioxide in the ocean and atmosphere, causing ocean acidification and creating a greenhouse effect (IPCC 2007). The change in ocean chemistry impedes the ability of corals to secrete calcium carbonate (Phinney 2006, Wild et al. 2011) and slows the growth of the crustose coralline algae (Anthony et al. 2008) that provide settlement cues for coral larvae, reducing overall coral recruitment success (Albright et al. 2010, Mason et al. 2011). Meanwhile, warming increases the frequency and variability of extreme weather events, leading to more coral bleaching episodes and subsequent disease outbreaks (Harvell et al. 1999, Jones et al. 2004, Harvell et al. 2007). The effects of the problems described above are synergistic (Knowlton and Jackson 2008). For example, excess nutrients can cause phytoplankton blooms followed by blooms of bacteria, respiration from which further increases the acidity of the water (Cai et al. 2011). Corals suffering from bleaching stress not only are more susceptible to disease attacks but also show reduced reproductive capacity (Szmant and Gassman 1990, Baird and Marshall 2002).

Recognizing the problem: the listing of *Acropora palmata* and other corals

Despite the inimical conditions facing corals, it is difficult to visualize that a coral population could be threatened with extinction. For fuzzy creatures, any countable number is devastating: There are just 21 wolves left in Oregon (U.S. Fish and Wildlife Service 2010). Instantly the very concept of wilderness is circumscribed, and our own fuzzy hairs bristle at the thought. But a coral? When told a coral species has decreased to 5% of its former abundance, are we nearly as concerned? After all, a coral can clone itself. It has indeterminate growth and its polyps don't naturally senesce (Jackson and Hughes 1985). In short, coral biology seems to preclude extinction.

Take, for example, the subject of this dissertation. The Atlantic elkhorn coral, *Acropora palmata*, was listed as threatened on the U.S. Endangered Species List in June 2006 based on a petition from the Center for Biological Diversity. The reason for listing was a 90-95% reduction in abundance throughout its range since the 1980s. The results outlined in the previous chapters confirm that the listing is warranted. Only one of five *A. palmata* populations we studied in the Caribbean is predicted to increase in size and percent cover in the foreseeable future. In the other four locations, if nothing is done, the population is predicted to disappear by the year 2030 (Chapter 4). These results are conservative, not taking into account the projected changes due to climate change (including possible increases in hurricane intensities) and other increases in anthropogenic stressors.

But what of other corals? If one-third of all reef-building corals are threatened with extinction (Carpenter et al. 2008), why are only the Caribbean acroporids listed as endangered on the US Endangered Species List? They may soon have plenty of company; as of late 2010, 82 additional coral species are being considered for inclusion. On the IUCN Red List, 32 corals are listed as endangered, and 234 are listed under the collective threatened categories (Vulnerable and worse). Therefore, the more appropriate question is, why were Caribbean acroporids *the first* corals to be listed? There are two plausible reasons: (1) it was easier to make the case that Caribbean acroporids are threatened, but many other coral species are equally threatened, or (2) Caribbean acroporids are disappearing more quickly than other coral species and are therefore more severely threatened with extinction than most coral species. Making this distinction has important implications for what we can expect in other coral populations in the future.

(1) *Acropora palmata* is easy to see, even from land. It lives on the shallowest reefs – the reef flat and the upper reef crest (0-5 m). Its fast growth and branching architecture lead to competitive dominance in these habitats. Its branch tips fragment easily, subsequently reattach to the substrate, grow vertically, and shade out potentially competing corals, which grow far more slowly. The same is true for its

also-listed Caribbean congener, *Acropora cervicornis*, which occupies a slightly deeper reef zone (5-20 m depth), or in more protected waters where it comes to the surface. Because these corals formed monocultures on the reefs for decades (e.g. Goreau 1959), their absence was striking, and they were relatively straightforward to quantify. It is easier to demonstrate a total absence of a formerly present species than to chart a scattered decline over decades, as would be necessary for other species.

(2) Alternatively, acroporids may have been first to be listed because their populations may actually be shrinking more rapidly than populations of other coral species. Clonal organisms evolved to inhabit relatively stable environments (Jackson and Hughes 1985). However, there is a spectrum among corals, from fast-growing and easily fragmented to slow-growing with a massive skeleton; this spectrum follows a depth gradient, from shallow, dynamic reefs to deep, stable reefs (Jackson and Hughes 1985). Elkhorn coral, as mentioned, inhabits the shallowest reefs, excluding virtually all other corals. This environment is characterized by constant strong wave action punctuated by rare and potentially catastrophic storms. Recovery from these storms necessitates some form of ecological resilience. Given that *Acropora palmata* is adapted to fragmentation in high-energy environments, colonies often have a high proportion of damaged or exposed tissue subject to stress. They evolved betting on a future in which exposed tissue could heal quickly; however, faced with increased sediments, sewage, algae, bacteria, disease, and acidity, that is no longer the case. This newfound lack of resilience is linked to the combined effects of multiple interacting

stressors and may explain why *Acropora palmata* is more susceptible to population decline than other corals.

If listing is due to (1), then all corals are just as unfortunate as *A. palmata*, and the listing procedure is catching up with our ability to recognize the problem. If (2) reflects reality, *Acropora* species are faring worse than other Caribbean species and deserve special conservation attention. The second explanation is more likely, as acroporids in general seem to be more vulnerable to bleaching (e.g. Carpenter et al. 2008) and predation (e.g. *Acanthaster* outbreaks in the Pacific (De'ath and Moran 1998). Finally, extinction of dominant corals is not unprecedented in the fossil record, and dominant species could be more prone to extinction than relatively rare species where habitat reduction is the primary cause of decline in abundance (Pandolfi 1999).

Resuscitating *Acropora palmata* populations

The question remains: Can *Acropora palmata* be brought back from the brink, and if so, how? If we do not address the three big environmental problems affecting coral reefs – overfishing, nutrient pollution, and carbon dioxide emissions – then the answer is no. But if we do address these issues, the answer may be yes, but only if we act quickly. But just how quickly? Perhaps as soon as 2030 (see Figure 2-3, Figure 4-6 for more detail).

Precisely because of its adaptations to an unstable environment, tolerance for survival as a small fragment, and fast growth, *Acropora palmata* is amenable to outplanting, as long as fragments are placed in conditions where they are capable of surviving. In fact, *Acropora cervicornis* has been outplanted in restoration projects in the Florida Keys since 2000. There are even private companies that “garden” these corals for hotels. In Florida, if we do nothing, the currently low level of benthic cover for *A. palmata* (4%) is projected to remain unchanged (Chapter 2). Fortunately, outplanting of *A. palmata* is being planned in Florida, and importantly, the number of outplants needed to make a positive change in *A. palmata* population dynamics is not outrageous. For example, if we secure 3000 20 cm wide outplants to the Florida Keys’ study area (1.3 colonies m^{-2}) annually for five years (from 2012-2017), benthic cover is projected to be a *minimum* of 20% by 2030 (Figure 2-3).

Outplanting projects could have synergistic scientific and conservation benefits. For example, outplanting provides researchers with an opportunity to determine whether population recovery might be further sped along by a suspected positive feedback on *Acropora palmata* density (compare density of 1000 versus 3000 outplants in 2030, Figure 2-3aii). If *A. palmata* does exhibit positive density dependence, the quantity of outplants needed or the number of years of outplanting required (and thus the total project cost) may be reduced significantly for the same conservation outcome. These data would inform not only future conservation decisions but also our basic understanding of coral population biology.

In addition to conducting outplanting projects at an ecologically meaningful scale, it will be crucial to employ the most appropriate and modern methods for monitoring population dynamics and population structure. Actively managed populations should be monitored using planar projection to facilitate translation between benthic cover, the standard metric of coral health, demographic surveys, and actual amount of tissue on the reef (Chapter 3). Finally, long-term species viability depends on the genotypic diversity of the population, which should be monitored over time.

Special considerations in endangered species management for clonal, colonial organisms

How is the recovery of a clonal, colonial organism distinct from that of an aclonal organism? There are three reasons it may be more difficult to recover clonal organisms than aclonal organisms. First, there is less than meets the eye. In other words, we do not know from surveys alone the number of genetically unique coral individuals (genets) in any given population (Baums et al. 2005a). We do know that it at a maximum is not larger than the number of non-contiguous adults and at a minimum is equal to 1. Therefore, a very large stand of corals may be as genetically fragile as a single colony. Coral bleaching and disease are known to affect coral genotypes unevenly, making genetic diversity within a reef tract a crucial component of coral population resilience (Baums et al. 2006). Because individual colonies self-fertilize only rarely (Baums et al. 2005b), multiple genotypes must be present for successful fertilization. As population size continues to diminish, the prospect for successful sexual fertilization (not including the naturally low probabilities associated with subsequent steps – larval survival, settlement, and recruitment to the benthos), is increasingly unlikely.

Second, threats to clonal species are often indirect. Terrestrial vertebrates, as well as fish populations, typically face extinction due to a combination of habitat loss and hunting. These threats are more direct and more easily mitigated than the typical list of threats facing clonal marine invertebrates. While reefs worldwide suffer from accidental ship groundings, and dynamite fishing persists in some parts of the world, Caribbean corals suffer primarily from indirect threats, as described above, that are more difficult to manage than direct threats such as overexploitation. There is often no single straightforward action that can be taken to reverse an indirect threat such as poor water quality, which can be due to agriculture, sewage, and industry. In addition, many indirect threats, such as those involving pollution and climate change, involve the actions of multiple countries and user groups. Reversing such threats requires complicated policy arrangements and the enforcement of international treaties and agreements.

Finally, alleviating the various threats suffered by corals would not produce immediate or even predictable results, and recovery may take years to notice. The response of a coral species to, say, improved water quality would be difficult to demonstrate if this action improved a coral's reproductive output but did not change its growth rate. Population dynamic models are less straightforward for clonal organisms than aclonal organisms; therefore, the success or failure of management decisions in coral populations may be far more difficult to assess at early stages of recovery. However, my thesis provides some insights into the strong potential of matrix-based approaches tailored to clonal species.

In contrast, there are two reasons why recovering a clonal organism such as a coral might be *less* difficult than recovering an aclonal organism: first, coral polyps are potentially immortal (Coates and Jackson 1985), which means that absolute extinction can be prevented with the proper protection. This also means that missing age classes may have less severe effects on population dynamics overall. Consider that some of the most massive coral species may live for hundreds of years. Thus, the failure to produce sufficient sexual recruits over the past 30 years does not automatically doom such a population to extinction. Similar to plants, corals may survive via asexual reproduction for decades until environmental conditions or density levels favor sexual reproduction once again. Thanks to this ability for reproductive bet-hedging, corals may be more difficult to drive to complete extinction. Second, individuals can reproduce via fragmentation a limitless number of times. While fragmented corals typically lose the ability to reproduce sexually below a certain total surface area (Szmant-Froelich 1985), the basic unit of the coral animal, the single polyp, is all that is required to regrow an entire colony. From very few starting individuals, an entire reef may be regrown. Coral population recovery is therefore not limited as severely by the factors that limit population recovery in fish and terrestrial vertebrates (e.g. gestation times, maximum brood sizes, sex ratio, and encounter rate between potential mates (Diaz-Pulido et al. 2009).

The number of corals has increased drastically on the IUCN Red List, and the number of corals on the U.S. Endangered Species List will likely increase soon as well. The unique life history characteristics of corals must be taken into careful consideration both when listing species as threatened and when designing a population recovery plan. The difference in body plan between a coral and a vertebrate needs to be addressed explicitly in the documentation declaring a coral as threatened. To help with listing, monitoring, and ultimately for recovery, endangered corals should be assessed with two metrics: percent of benthic cover and genotypic diversity. Foremost, cover as a percentage of benthic substrate (percent cover) should be used as a metric to assess population status and to determine recovery goals. This metric establishes a connection between the organism and the critical role it plays in building the reef. This metric can be used in addition to counts of non-contiguous individuals, which are still an important measure for many coral species. Concurrently, genotypic diversity must be measured as a baseline and monitored over time to ensure long-term evolutionary viability (Hemand and Vollmer 2010). Without information on both percent cover and genetic diversity, conservation practitioners will have no way to accurately judge the recovery potential of a population or diagnose recovery failures. While the unique life history characteristics of corals present additional challenges for effective conservation and population recovery, the survey methodology and genetic analysis techniques needed to meet this challenge already exist. At this point, we are simply missing the appropriate language in our legislation.

Save the corals

There are several reasons why facilitating the recovery of *Acropora palmata* and corals in general is worthwhile. The importance of species is the subject of entire books (Kareiva and Levin 2003). To many, no further motivation for conservation is needed beyond a belief in the fundamental value of each species. A different perspective is taken by those who believe a species should be preserved if it has an important and demonstrable ecological function. Because corals are not just important to coral reef ecosystems but are also the very engineers and builders of these ecosystems, their preservation as a group is justified by their fundamental, crucial role in creating coral reef ecosystems. When an ecosystem function is served by only one species, its ecological value becomes greater. *Acropora palmata* alone forms the shallowest Caribbean reefs. There are no functionally redundant, or “backup”, species ready to fill this role should it go extinct. It alone provides the complex branching architecture that creates homes, refuges, and less turbulent habitats for countless organisms in the shallows (Lirman 1999). Thus, this species deserves its high conservation priority. Declaring a coral’s existence value or ecological value is a reason to conserve it, but without recovering ecological function by restoring its abundance to historical levels, its only ecological value will be on paper.

REFERENCES

Albright, R., B. Mason, M. Miller, and C. Langdon. 2010. Ocean acidification compromises recruitment success of the threatened Caribbean coral *Acropora palmata*. Proceedings of the National Academy of Sciences of the USA 107:20400. One page only??

Anthony, K. R. N., D. I. Kline, G. Diaz-Pulido, S. Dove, and O. Hoegh-Guldberg. 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. Proceedings of the National Academy of Sciences of the USA 105:17442. One page only?

Baird, A. H., and P. A. Marshall. 2002. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Marine Ecology Progress Series 237:133-141.

Barott, K., J. Smith, E. Dinsdale, M. Hatay, S. Sandin, and F. Rohwer. 2009. Hyperspectral and physiological analyses of coral-algal interactions. Plos One 4:e8043.

Baums, I. B., M. W. Miller, and M. E. Hellberg. 2005a. Regionally isolated populations of an imperiled Caribbean coral, Acropora palmata. Molecular Ecology 14:1377–1390.

Baums, I. B., C. R. Hughes, and M. E. Hellberg. 2005b. Mendelian microsatellite loci for the Caribbean coral Acropora palmata. Marine Ecology Progress Series 288:115–127.

Baums, I. B., M. W. Miller, and M. E. Hellberg. 2006. Geographic variation in clonal structure in a reef-building Caribbean coral, *Acropora palmata*. Ecological Monographs 76:503-519.

Burkepile, D. E., and M. E. Hay. 2009. Nutrient versus herbivore control of macroalgal community development and coral growth on a Caribbean reef. Marine Ecology Progress Series 389:71-84.

Cai W-J., X. Hu, W.J. Huang, M.C. Murrell, J.C. Lehrter, S.E. Lohrenz, W.C. Chou, W. Zhai, J.T. Hollibaugh, Y. Wang, et al. 2011. Acidification of subsurface coastal waters enhanced by eutrophication. Nature Geoscience 4:766–770.

Carpenter K.E., M. Abrar, G. Aeby, R.B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortes, J.C. Delbeek, L. DeVantie, et al. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321:560–563.

Coates, A., and J.B.C. Jackson. 1985. Morphological themes in marine invertebrates *in* J.B.C. Jackson, L. Buss, and R. Cook (Eds.). Population biology and evolution of clonal organisms. Yale University Press, New Haven. 530pp.

De'ath, G., and P. Moran. 1998. Factors affecting the behaviour of crown-of-thorns starfish (*Acanthaster planci* L.) on the Great Barrier Reef: 2: Feeding preferences. Journal of Experimental Marine Biology and Ecology 220:107–126.

Diaz-Pulido, G., L. J. McCook, et al. 2009. Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. PLoS ONE 4: e5239.

Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. Marine Pollution Bulletin 50:125-146.

Gardner, T. A. 2003. Long-Term Region-Wide Declines in Caribbean Corals. Science 301:958–960.

Garren, M., S.P. Smriga, and F. Azam. 2008. Gradients of coastal fish farm effluents and their effect on coral reef microbes. Environmental Microbiology 10:2299-2312.

Haas, A. F., C. Jantzen, M. S. Naumann, R. Iglesias-Prieto, A. F. Haas, C. Jantzen, M. S. Naumann, R. Iglesias-Prieto, and C. Wild. 2010. Organic matter release by the dominant primary producers in a Caribbean reef lagoon: Implication for in situ O_2 availability. Marine Ecology Progress Series 409:27-39.

Harvell, C. D., K. Kim, J. M. Burkholder, R. R. Colwell, P. R. Epstein, D. J. Grimes, E. E. Hofmann, E. K. Lipp, A. D. Osterhaus, R. M. Overstreet, J. W. Porter, G. W. Smith, and G. R. Vasta. 1999. Emerging marine diseases - Climate links and anthropogenic factors. Science 285:1505-1510.

Harvell, D., E. Jordán-Dahlgren, S. Merkel, E. Rosenberg, L. Raymundo, G. Smith, E. Weil, and B. Willis. 2007. Coral disease, environmental drivers, and the balance between coral and microbial associates. Oceanography 20:172-195.

Hemond, E. M., and S. V. Vollmer 2010. Genetic diversity and connectivity in the threatened staghorn coral *Acropora cervicornis* in Florida. PLoS One 5:e8652.

IPCC. 2007. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Pachauri, R.K. and Reisinger, A. (Eds.) Geneva, Switzerland. 104 pp.

Jackson J., Hughes T.P. 1985. Adaptive strategies of coral-reef invertebrates. American Scientist 73:265–274.

Jackson, J. B. C. 1997. Reefs since Columbus. Coral Reefs 16 (suppl.):S23-S32.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-638.

Jones, R. J., J. Bowyer, O. Hoegh-Guldberg, and L. L. Blackall. 2004. Dynamics of a temperature-related coral disease outbreak. Marine Ecology Progress Series 281:63-77.

Kareiva P.M. and S.A. Levin. (Eds.) 2003. The importance of species. Princeton Univ Press. 427 pp.

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

Klaus, J. S., I. Janse, J. M. Heikoop, R. A. Sanford, and B. W. Fouke. 2007. Coral microbial communities, zooxanthellae and mucus along gradients of seawater depth and coastal pollution. Environmental Microbiology 9:1291-1305.

Knowlton, N., and J. B. C. Jackson. 2008. Shifting Baselines, Local Impacts, and Global Change on Coral Reefs. PLoS Biology 6:e54.

Koop, K., D. Booth, A. Broadbent, J. Brodie, D. Bucher, D. Capone, J. Coll, W. Dennison, M. Erdmann, and P. Harrison. 2001. ENCORE: The effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. Marine Pollution Bulletin 42:91-120.

Lirman D. 1999. Reef fish communities associated with *Acropora palmata*: Relationships to benthic attributes. Bulletin of Marine Science 65:235–252.

Mason B., M. Beard, M.W. Miller. 2011. Coral larvae settle at a higher frequency on red surfaces. Coral Reefs 30:667–676.

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

Newman, M. J. H., G. A. Paredes, E. Sala, and J. B. C. Jackson. 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. Ecology Letters 9:1216-1227.

Nugues, M. M., G. W. Smith, R. J. Hooidonk, M. I. Seabra, and R. P. M. Bak. 2004. Algal contact as a trigger for coral disease. Ecology Letters 7:919-923.

Pandolfi, J. M. 1999. Response of Pleistocene Coral Reefs to Environmental Change Over Long Temporal Scales. Integrative and Comparative Biology 39:113–130.

Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955-958.

Phinney, J. T. 2006. Coral reefs and climate change : Science and management. American Geophysical Union, Washington, DC.

Rasher, D. B., and M. E. Hay. 2010. Chemically rich seaweeds poison corals when not controlled by herbivores. Proceedings of the National Academy of Sciences 107:9683-9688.

Rohwer, F., and M. Youle. 2010. Coral Reefs in the Microbial Seas. Plaid Press. 201pp.

Selig, E. R., and J. F. Bruno. 2010. A global analysis of the effectiveness of marine protected areas in preventing coral loss. PLoS ONE 5:e9278.

Smith, J. E., M. Shaw, R. A. Edwards, D. Obura, O. Pantos, E. Sala, S. A. Sandin, S. Smriga, M. Hatay, and F. L. Rohwer. 2006. Indirect effects of algae on coral: Algae-mediated, microbe-induced coral mortality. Ecology Letters 9:835-845.

Sutherland, K. P., J. W. Porter, J. W. Turner, B. J. Thomas, E. E. Looney, T. P. Luna, M. K. Meyers, J. C. Futch, and E. K. Lipp. 2010. Human sewage identified as likely source of white pox disease of the threatened Caribbean elkhorn coral, *Acropora palmata*. Environmental Microbiology 12:1122–1131.

Szmant-Froelich, A. M. 1985. The effect of colony size on the reproductive ability of the Caribbean coral *Montastraea annularis*. Proceeding of the 5th International Coral Reef Congress. 4:295-300.

Szmant, A. M., and N. J. Gassman. 1990. The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. Coral Reefs 8:217-224.

U.S. Fish and Wildlife Service. 2010. Website: http://www.fws.gov/midwest/wolf/aboutwolves/WolfPopUS.htm. Accessed Oct 10, 2011.

Wild C., Hoegh-Guldberg O., Naumann M., Colombo-Pallotta M.F., Ateweberhan M., Fitt W.K., Iglesias-Prieto R., Palmer C., Bythell J.C., Ortiz J.-C., et al. 2011. Climate change impedes scleractinian corals as primary reef ecosystem engineers. Marine and Freshwater Research 62: 205–215.

Williams, D. E., and M. W. Miller. 2006. Coral disease outbreak: pattern, prevalence and transmission in *Acropora cervicornis*. Marine Ecology-Progress Series 301: 119–128.