EFFECTS OF CHANGING TEMPERATURES ON CORAL REEF HEALTH: IMPLICATIONS FOR MANAGEMENT

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A dissertation submitted to the faculty of the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Curriculum in Ecology

Chapel Hill
2008

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ABSTRACT

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Effects of changing temperatures on coral reef health: implications for management
(Under the direction of John Bruno)

Human-induced climate change has already led to substantial changes in a variety of ecosystems. Coral reefs are particularly vulnerable to rises in ocean temperature as a result of climate change because they already live near their thermal limits. However, we know little about the spatial patterns of temperature anomalies, areas of greater than usual temperature, which cause coral mortality and increased rates of coral disease. These gaps in knowledge make it difficult to design effective management strategies for mitigating the effects of ocean warming. My dissertation research uses a combination of a new satellite ocean temperature dataset, field surveys on coral health, and data on marine protected area (MPA) boundaries to analyze how ocean temperatures are affecting coral reef health at regional and global scales. I discovered that temperature anomalies are spatially and temporally variable from 1985-2005 even during El Niño events. They are also typically less than 50 km², smaller than the resolution of many climate models. In addition, I found a strong relationship on the Great Barrier Reef between the number of temperature anomalies and the number of cases of white syndrome, a prevalent coral disease. Results from this study suggest that temperature anomalies are playing a major role in the observed decline of coral reefs over the last 30-40 years. This decline highlights the importance of determining whether MPAs, one of the most common management tools are effective in restoring coral
cover. My analyses demonstrated that MPAs can confer some ecosystem resilience through fisheries management and land management practices at regional scales. Coral cover on reefs inside of MPAs did not change over time, while unprotected reefs experienced declines in coral cover. However, MPAs do not moderate the effect of thermal stress on corals or reduce coral decline at rates that can offset losses from thermal stress and other major natural and human-caused disturbances. MPAs are clearly a key tool in the management of fisheries and coral reef health. My dissertation research underscores the need for both MPAs and additional measures aimed at reducing the anthropogenic activities driving climate change.
DEDICATION

To my grandfather, my dear Papa,
who was with me every step believing in me
ACKNOWLEDGEMENTS

To my advisor, John Bruno, whose enthusiasm, optimism, and passion for science has inspired me to do my best and grow as a scientist.

To my committee, I have benefited greatly from your support and constructive criticism over the years. To Judy Lang for traveling so far and always being willing to engage in a good debate, Peter White for helping me see life through the music of Bob Dylan and the poetry of Robert Frost, Charles Mitchell for always having an open door and mind, and Aaron Moody for helping me see a different view of the world.

I am particularly grateful to the EPA STAR Fellowship program, whose support enabled me to focus on my research for three years. I am also extremely thankful for the generosity of Dr. M. Ross and Mrs. Charlotte Johnson for endowing my Royster Society of Fellows Dissertation Completion Fellowship. Both of these fellowships gave me opportunities to experience things I otherwise would have missed.

To the countless volunteers and scientists who surveyed reefs over the last 40 years, I owe a great debt of gratitude to for all of your hard work, which has made my analyses possible.
I owe a huge gratitude of debt to my labmates who were there for the duration – Mary O'Connor and Sarah Lee. They provided a rich intellectual environment that helped me become a better scientist. They were great friends and always made me see the humor in sometimes difficult times. I was continually awed by their strength, determination, creativity, and incredible science. And to the Bruno Lab of the future: Pamela Reynolds and Andrea Anton, thank you for your help and support.

To the incredible technicians and friends who have supported me and the Bruno Lab over the years: Johanna Kertesz (the best running partner at 6 am), Meredith Kintzing, Laura Ladwig, and Jessica Wall. A special thanks to Virginia Schutte for all of her help and her fantastic sense of humor.

To Ken Casey at NOAA, who made collaboration a joy. I am grateful for your friendship and all that you have taught me.

To the Department of Marine Sciences for giving me a home these last several years and especially to Nadera Malika-Salaam and Mary Campbell for always being willing to provide a helping hand, many thanks for your support.

To Robert Peet, Denise Kenney, and Jack Weiss, who were great resources for me and help to make the Curriculum in Ecology a wonderful environment for graduate students.
To my dear friends in Marine Sciences and the Curriculum in Ecology for their support and friendship: Alfredo Lopez de Aretxabaleta, Catherine Edwards, Patrick Gibson, Karen Lloyd, David Luther, Matthew McKown, Meghan McKnight, Howard Mendlovitz, Andrew Steen, and Christy Violin.

To my family outside of Chapel Hill, particularly my mother Meg Selig, my "aunts" Ellen and Beth Rashbaum, and my aunt Kate Kimelman, who have supplied me with care packages and love through the duration of this process. I lost two very important family members during these years, my grandfather Philip Rashbaum and my great aunt Dorothy Helfeld. They helped me become who I am and their memories are a blessing.

I feel especially thankful to my family in Chapel Hill, my rocks during tough times, my great aunt Eleanor Sorgman, my amazing and inspiring sister Heather Ragan, my wonderful niece Ariel Kwayke and the best bike mechanic of all time, Jason Merrill. To Trond Kristiansen, whose encouragement and support helped me through to the finish.

To Shirin Ardakani, the greatest of friends, my second sister, your friendship means the world to me.

To my family of friends scattered near and far: Eliza Beardslee, Linda Cotton, Rachel Galper, Amanda Marcus, Susan Minnemeyer, Hannah Purdy, and Kay Sterner. They have been my other family and provided places of refuge, unflagging love, and support.
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INTRODUCTION

Studies in a wide range of ecosystems have found that climate change has already had or is predicted to have far-reaching effects (Vitousek et al. 1997; Walther et al. 2002). Documented biological responses to climate change include shifts in species ranges (Barry et al. 1995; Parmesan & Yohe 2003; Precht & Aronson 2004), phenological patterns (Menzel & Fabian 1999; Parmesan & Yohe 2003; Root et al. 2003), and community structure due to varied climate effects at different trophic levels (Schmitz et al. 2003; Voigt & al. 2003). Our ability to document or forecast these biological responses to climate change is impeded by several gaps in knowledge. The spatial and temporal variability of key climatic parameters like temperature, which drive ecosystem changes, remain poorly understood, particularly in the oceans at ecologically relevant scales. In addition, physical data are rarely linked with biological data to build an integrated framework for analyzing how climate change is affecting ecosystems regionally (but see Beaugrand et al. 2003; Behrenfeld et al. 2006). Understanding these relationships is particularly important for designing and evaluating appropriate management interventions. My dissertation uses spatially explicit databases to examine how tropical ocean temperature variability affects coral health, and whether management strategies like marine protected areas can mitigate the effects of climate change.

Reef-building or scleractinian corals are widely recognized as particularly vulnerable to climate warming because of their thermal sensitivity (Coles et al. 1976; Hughes et al. 2003; Sheppard 2003). Scleractinian corals are the foundation species of coral reefs (Bruno
one of the most diverse ecosystems in the world (Reaka-Kudla 1997; Roberts et al. 2002). Globally, these ecosystems have undergone rapid, extensive changes during the last 20-30 years. On some reefs, these changes are unprecedented in the Holocene paleontological record (Aronson & Precht 2001; Wapnick et al. 2004; but see Hubbard et al. 2005). Declines have been extensive, affecting a wide range of taxa in both protected and unprotected areas (Rogers & Beets 2001; Edmunds 2002; Bellwood et al. 2004). One of the most commonly used metrics for evaluating coral health is the percentage of live coral tissue covering the hard reef substratum. In the Caribbean, average hard coral cover has decreased from approximately 50% in the late 1970s (Gardner et al. 2003) to 17% in 2005 (Schutte et al. in prep). Similar declines have occurred in the Indo-Pacific, where regional averages in 2003 were 22% (Bruno & Selig 2007). Even on well-managed reefs like the Great Barrier Reef, average coral cover has decreased from 40% in the 1960s to 20% in 2000 (Bellwood et al. 2004).

The global and indiscriminate nature of the decline in coral cover is at least partially attributable to increases in ocean temperature as a result of climate change (Hoegh-Guldberg 1999). Climate change is expected to continue to have devastating effects on coral reef ecosystems due to rising sea level (Blanchon & Shaw 1995), ocean circulation changes (Harley et al. 2006), further increases in ocean temperature (Sheppard 2003; McWilliams et al. 2005), and ocean acidification (Hoegh-Guldberg et al. 2007). In the short-term, increases in ocean temperature have had some of the most visible and dramatic effects because they are drivers of two major causes of coral mortality: coral disease and coral bleaching (Arceo et al. 2001; Aronson & Precht 2006; Graham et al. 2006).
Coral bleaching is perhaps the most widely known and documented effect of ocean warming. Bleaching describes the separation of the algal symbionts, known as zooxanthellae, from the coral host. Typically, bleaching occurs when temperatures exceed the local average summertime maximum temperature by approximately 1°C (Glynn 1993). Bleaching is a natural stress response (Glynn 1993) and corals can recover from bleaching episodes (Glynn 1993; Brown 1997). However, when temperature magnitudes are too high or prolonged, bleaching can cause coral mortality (Glynn 1993). Mass or large-scale bleaching events due to severe El Niño events in 1982-1983 and 1997-1998 were coincident with major regional coral mortality (Glynn et al. 1988; Wilkinson 2000; Bruno et al. 2001; Glynn et al. 2001). Models predict that warming ocean temperatures as a result of climate change will increase the number and severity of these mass bleaching events (Hoegh-Guldberg 1999; Sheppard 2003; McWilliams et al. 2005; Sheppard & Rioja-Nieto 2005).

The relationship between ocean temperature and coral disease is less well understood. Coral diseases have caused significant mortality in the last 30 years, particularly in the Caribbean, where white band disease decimated acroporid populations (Aronson & Precht 2001). Recent work suggests that rises in ocean temperatures may be partially responsible for the emergence of new diseases and increases in disease reports (Sutherland et al. 2004; Ward & Lafferty 2004; Bruno et al. 2007). Warmer temperatures have been associated with faster pathogen development for several coral diseases (Alker et al. 2001; Richardson & Kuta 2003). In addition, field studies have documented summertime increases in the number of cases for a variety of coral diseases (Kuta & Richardson 2002; Patterson et al. 2002; Jones et al. 2004; Willis et al. 2004; Boyett et al. 2007).
Mitigating the effects of coral decline as a result of coral disease and bleaching represents a major management challenge. A substantial success in marine ecosystem management has been the use of marine protected areas (MPAs) to restore the abundance of targeted populations in both temperate and tropical ecosystems (Babcock et al. 1999; Murawski et al. 2000; Halpern 2003; Russ et al. 2004). Several studies in coral reef ecosystems have documented increases in fish abundance inside MPAs and spillover effects to neighboring fisheries (McClanahan & Mangi 2000; Roberts et al. 2001; Evans & Russ 2004). Successful fisheries management and the subsequent restoration of a more complete trophic structure through protection in MPAs is now proposed as a possible mechanism for indirectly increasing resilience to climate change (Hughes et al. 2003; Mumby et al. 2006; Mumby et al. 2007a). Although MPAs cannot directly affect temperature, they are hypothesized to increase resilience to thermal events by reducing other stressors like overfishing or terrestrial run-off (Grimsditch & Salm 2005; Wolanski & De'ath 2005; Hughes et al. 2007). After bleaching or disease events, bare substrate can be colonized by macroalgae, which prevents coral recruitment (Diaz-Pulido & McCook 2002; Birrell et al. 2005). Increased herbivory on reefs can prevent a shift to macroalgal dominance by maintaining space for coral recruitment and growth (Hughes et al. 2007; Mumby et al. 2007a; Mumby et al. 2007b). In spite of these potential benefits, the large-scale effects of MPAs on corals are not well understood. A lack of awareness about their limitations could undermine future efforts to establish MPAs, especially in the face of some failures. In addition, the intense focus on MPAs could fail to catalyze political will around other necessary policy efforts.
Although climatic changes affect ecosystems at local scales, we need to understand variability in temperature at regional and global scales to make predictions about future ecosystem changes and design effective management strategies. The cornerstone of my dissertation was the development of a 4-km coral reef temperature anomaly database (CoRTAD), which calculated anomalies globally from 1985-2005. I used these data to explore the spatial and temporal variability in the temperature anomalies driving coral decline through bleaching and disease. By coupling these temperature data with field survey data on white syndrome, a coral disease causing mortality of key coral taxa on the Great Barrier Reef, I was able to determine that the number of temperature anomalies was positively related to disease frequency. The results of these analyses highlighted the need to explore whether MPAs could be an effective tool for reducing coral decline. Initially, I addressed this question with spatial data on MPA boundaries and surveys of live coral cover from around the world. Then I integrated spatial data on MPA boundaries with the temperature anomaly database to analyze whether management through MPAs could be an effective strategy for reducing the effects of temperature stress. Together this work described how warmer temperatures are affecting coral reef health at broad spatial scales and what strategies may be necessary for reversing coral decline.

Chapter 1: Mapping the variability in frequency, magnitude and spatial extent of coral reef temperature anomalies between 1985 and 2005

In spite of the evidence that temperature anomalies play a fundamental role in coral reef health, their spatial and temporal patterns have not been analyzed. I used the CoRTAD
to quantify key anomaly characteristics including anomaly frequency, magnitude, duration, and area across years and regions. I found substantial fine-scale regional and local variability in these parameters, which suggests that temperature-related disease and bleaching is likely to be highly patchy. I calculated that 48% of bleaching-related and 44% of disease-related anomalies were less than 50 km², smaller than the resolution of most models used to forecast climate changes. Understanding the link between the scale of temperature data and biological processes will facilitate the design of appropriate management strategies and accurate predictions about the impacts of climate change on coral reef ecosystems.

Chapter 2: Analyzing the relationship between ocean temperature anomalies and coral disease outbreaks at broad spatial scales

Rising terrestrial and ocean temperatures have been hypothesized to cause the emergence of new diseases and increase the frequency and severity of known diseases (Harvell et al. 1999; Harvell et al. 2002). However, the temperature thresholds relevant to most coral disease outbreaks are not known. In Chapter 2, I used the temperature anomaly database created in Chapter 1 and a long-term disease database from the Australian Institute for Marine Science (AIMS) to determine which temperature thresholds best describe changes in disease frequency. In addition, I tested whether the number of temperature anomalies was related to an outbreak of a coral disease, white syndrome, on the Great Barrier Reef in 2002. The weekly sea surface temperature anomaly (WSSTA) metric, which defined an anomaly as being at least 1°C more than the typical 21-year average temperature of a specific week, best explained the relationship between anomaly frequency and white syndrome cases. The relationship between the number of these temperature anomalies and white syndrome cases
was highly significant. In addition, there was a significant, nearly exponential relationship between total coral cover and the number of disease cases. Together, coral cover and WSSTAs explained nearly 75% of the variance in disease cases and both high coral cover and WSSTAs were necessary for triggering disease outbreaks (Selig et al. 2006). These results suggest that disease may become a key driver of coral mortality as a result of increased ocean temperatures associated with the climate change.

Chapter 3: Evidence of increased resilience to corals from marine protected areas

Marine protected areas (MPAs) are known to be effective for managing fisheries (Alcala et al. 2005; McClanahan et al. 2007). MPAs are thought to be able to benefit corals indirectly either through restoring historic food web structure or by mitigating nutrient and sediment run-off if the MPA includes a terrestrial component (Russ et al. 2004; Wolanski et al. 2004; Mumby et al. 2006). I tested the hypothesis that MPAs can have a positive effect on coral cover by developing spatial databases of MPAs and more than 9000 surveys of live coral cover from 1969-2006 from peer-reviewed literature, grey literature, and publicly available datasets like Reef Check (www.reefcheck.org). I then analyzed whether the relationship between protection and the rate of coral cover change varied with the age of the MPA at the time of the survey. Coral cover in MPAs did not change over time whereas coral cover on unprotected reefs declined. The benefit from MPAs generally increased with the number of years of protection. In the Caribbean, this trend continued until a leveling-off at approximately 30 years of protection. On the other hand, there were two distinct trend dynamics in the Indo-Pacific. Initially the change in coral cover was positive, but then was reset to a trend that was not significantly different from zero after 20-30 years of protection.
These two trends in coral cover reflect trajectories before and after the 1998 El Niño event, which suggest that the effects of major thermal disturbances may not be mitigated by protection. Although my work demonstrated a resilience effect, it also highlighted the limitations of MPAs to restore coral cover to historic levels.

Chapter 4: Temperature-driven coral decline: do marine protected areas have a role?

Results from Chapter 3 indicated that the resilience effect of MPAs may not explicitly moderate the effect of temperature stress on coral cover. I tested whether MPAs were successfully reducing the impact of thermal stress on coral cover and quantified how temperature anomalies were generally affecting coral cover using the temperature database constructed in Chapter 1 and the MPA and live coral cover databases used in Chapter 3. MPAs did not modify the effect of temperature anomalies on coral cover over time. In addition, the magnitude of the benefit of MPAs generally was not enough to compensate for the negative effect of temperature anomalies on coral cover. These results suggest that MPAs will not be able to counteract the impacts of increased thermal stress as a result of climate change.

Overall Synthesis

The results of my dissertation work suggest that temperature anomalies are playing a major role in the decline of coral reefs and that protection in MPAs alone will not be sufficient to mitigate coral decline. Coral reef conservation has been limited by a lack of understanding of the stressors responsible for coral reef decline. My work suggests that temperature-driven coral bleaching and disease are major drivers of coral loss. In addition, I
demonstrated that MPAs can confer some ecosystem resilience through fisheries management and land management practices at regional scales. However, MPAs do not reduce coral decline at rates that can offset losses from thermal stress and other major natural and human-caused disturbances. MPAs are obviously a key tool in the management of fisheries and coral reef health. Nonetheless, my work underscores the need for additional and more direct conservation measures aimed at reducing the anthropogenic activities driving climate change.
References


CHAPTER 1

Mapping the variability in frequency, magnitude and spatial extent of coral reef temperature anomalies between 1985 and 2005

Abstract

Increases in ocean temperature due to climate change are expected to have extensive impacts on marine ecosystems. Coral reefs are widely considered to be particularly vulnerable to these changes in ocean temperatures, yet we understand little about the broad-scale spatiotemporal patterns and fine-scale variability in ocean temperatures underlying many coral reef ecosystem changes. We created a novel 4-km global ocean temperature anomaly database to measure these temperature patterns on coral reefs. Then we tested whether key characteristics in temperature anomalies, including their size and spatial extent, varied regionally and annually. Our analyses found substantial variability in anomaly frequency, duration and magnitude across and within tropical regions. We also discovered that even during major climatic events like El Niños, locations affected by these anomalies were idiosyncratic. In addition, we found that 48% of bleaching-related, and 44% of disease-related, anomalies were less than 50 km$^2$, smaller than the resolution of most models used to forecast climate changes. These analyses describe a striking degree of fine-grained variability in temperature anomalies. Quantifying this variability is essential to our ability to
understand the scales at which temperature is affecting coral reef ecosystem health and to make accurate predictions about the potential impacts of climate change.

Introduction

Human-induced climate change is altering the physical processes that structure natural communities (Chapin et al. 2000; Parmesan & Yohe 2003; Thomas et al. 2004; Harley et al. 2006). Indeed, climate change is expected to continue to have wide-ranging effects on marine ecosystems due to warming ocean temperatures, sea level rise, ocean acidification, and changes in ocean circulation patterns (IPCC 2007). Differences in these physical properties could affect species ranges, species composition and diversity, and productivity (Harley et al. 2006), which could lead to major social and economic consequences (Stern 2006). Although we are already seeing evidence of climate change effects on a range of ecosystems, we still do not fully comprehend how the underlying physical patterns being modified by climate change are linked with biological patterns (Walther et al. 2002). Without understanding the interaction between physical patterns and biological responses, we cannot accurately predict ecosystem responses to climate change or develop the necessary management interventions.

Globally, ocean surface temperatures have increased 0.52°C ± 0.19°C from 1850 to 2004 (Rayner et al. 2006). Ocean temperature changes can have a range of impacts on marine species from physiological stress to mortality (Harley et al. 2006). Climate models predict global rises in ocean temperature over at least the next 100 years (Rayner et al. 2006; IPCC 2007). Coincident with anthropogenically driven ocean warming are predicted
increases in the severity of ocean temperature anomalies, defined as periods of unusually warm ocean temperatures, in all of the tropical oceans (Hoegh-Guldberg 1999; Sheppard 2003; Sheppard & Rioja-Nieto 2005). Although temperature anomalies can be a natural consequence of climate variability, recent work has indicated that the recent thermal event in the Caribbean in 2005 was at least partially due to anthropogenic climate changes (Donner et al. 2007).

Scleractinian or reef-building corals are believed to be particularly vulnerable to these temperature anomalies because they already live near their thermal limits (Jokiel & Coles 1990; Glynn 1993; Berkelmans & Willis 1999). Warmer than usual temperatures play a role in two processes that can lead to coral mortality: coral bleaching and disease. Mortality from bleaching and disease is known to be a major cause of the unprecedented decline in coral reef health in the last 30 years in both the Caribbean (Gardner et al. 2003) and Pacific (Bruno & Selig 2007). Coral bleaching has become more frequent and more extensive in the last twenty years (Hoegh-Guldberg 1999). Mass bleaching due to severe El Niño events in 1982-1983 and 1997-1998 led to exceptional regional-scale coral mortality (Glynn et al. 1988; Wilkinson 2000; Bruno et al. 2001; Glynn et al. 2001). In order to predict the consequences of future thermal stress events and design effective management actions, we need to quantify the temperature patterns causing these coral declines.

Long-term sea surface temperature datasets have provided valuable historical records of temperature patterns in coral reef systems (Folland et al. 2001; Rayner et al. 2006). These data have also been used to model possible increases in the temperature anomalies on coral reefs and put current temperatures in a climate context (Sheppard 2003; Barton & Casey 2005; Sheppard & Rioja-Nieto 2005). However, these datasets have resolutions of 100 km or
more, which may be too coarse to pair with biological data and ecological processes if there is substantial fine-grained variability (Sheppard 2003; Sheppard & Rioja-Nieto 2005). Patterns in coral abundance and diversity can vary at scales of 1-10 km (Edmunds & Bruno 1996) and ecological processes like dispersal similarly occur at scales of 1-10s of kilometers for many coral reef organisms (Grantham et al. 2003; Ayre & Hughes 2004). Therefore, we need to understand the scale of variability in temperature anomalies to determine how best to match biological and temperature data on coral reefs.

We quantified the spatial and temporal patterns of temperature anomalies associated with bleaching and disease using a novel 4-km global ocean temperature anomaly database from 1985-2005. First we calculated three parameters of temperature anomalies that relate to generally accepted metrics of disturbance: frequency, magnitude, and duration (Connell 1978). These data not only enabled us to establish a baseline from which we could compare extreme events like the 1998 El Niño, but also allowed us to test how these anomaly characteristics varied by region. Because disturbance extent and spatial scale are also important determinants of severity and are often used in the design of protected areas, we measured these variables as well (Connell 1978; Pickett & Thompson 1978). By calculating the total area affected by anomaly events and quantifying the distribution of anomaly sizes, we evaluated the degree of clustering of anomalies and whether they were spatially pervasive or localized over large spatial scales. Together, these analyses described the spatial structure and variability of temperature anomalies, the results of which provide critical context for evaluating past and future thermal stress patterns.
Materials and Methods

Temperature dataset

The Coral Reef Temperature Anomaly Database (CoRTAD) was developed using data from the Pathfinder Version 5.0 collection produced by the National Oceanic and Atmospheric Administration’s (NOAA) National Oceanographic Data Center (NODC) and the University of Miami’s Rosenstiel School of Marine and Atmospheric Science (http://pathfinder.nodc.noaa.gov). These data are derived from the Advanced Very High Resolution Radiometer (AVHRR) sensor and are processed to a resolution of approximately 4.6 km at the equator. These data have the highest resolution covering the longest time period of any satellite-based ocean temperature dataset (Fig. 1.1).

We used weekly averages of day and nighttime data with a quality flag of 4 or better, which is a commonly accepted cutoff for “good” data (Casey & Cornillon 1999; Kilpatrick et al. 2001). By using a day-night average, we reduced the number of missing pixels by 25% with virtually no loss in accuracy (Table S1.1). We also added back in some data that were initially given low quality levels. The Pathfinder algorithm eliminates any observation with a Sea Surface Temperature (SST) more than 2°C different from a relatively coarse resolution SST value based on the Reynolds Optimum Interpolation Sea Surface Temperature (OISST) value, a long-term, in situ-based data set (Kilpatrick et al. 2001; Reynolds et al. 2002). Therefore, we added observations back into the analysis if the SST was greater than the OISST, but less than the OISST+5°C. The 5°C threshold is a reasonable selection that allows diurnal warming events (Kawai & Wada 2007) or other spatially limited warm spots back into the dataset without including unrealistic and erroneously warm values. Values less than the OISST were not included because they may have been biased by cloud
contamination and other satellite errors, which tend to result in cooler SST estimates. These processes resulted in a dataset with only 21.2% missing data.

To create a gap-free dataset for analysis, we used 3 x 3 pixel median spatial fill. We then did a temporal fill using the Piecewise Cubic Hermite Interpolating Polynomial (PCHIP) function in Matlab (The Mathworks Inc. 2006) to fill the remaining gaps. We chose this conservative approach because it provided interpolated SSTs that are bounded by the nearest available values in time. It also used data from only a very limited spatial domain, which is an important consideration given the variability of coral reef environments. Using these gap-filled data, we then created site-specific climatologies for each reef grid cell to describe long-term temperature patterns over the 21-year dataset (Eqn. 1). The climatology was generated using a harmonic analysis procedure that fits annual and semi-annual signals to the time series of weekly SSTs at each grid cell:

\[
\text{SST}(t)_{\text{clim}} = A \cos(2\pi t + B) + C \cos(4\pi t + D) + E
\] (1)

where \( t \) is time, \( A \) and \( B \) are coefficients representing the annual phase and amplitude, \( C \) and \( D \) are the semi-annual phase and amplitude, and \( E \) is the long-term temperature mean.

Similar approaches have been used for generating climatologies because they are more robust than simple averaging techniques, which can be more susceptible to data gaps from periods of cloudiness (Podesta et al. 1991; Mesias et al. 2007).

Sea surface temperatures from AVHRR quantify only the temperature of the 'skin' of the ocean, roughly the first 10 \( \mu \)m of the ocean surface (Donlon et al. 2007). Most field surveys of coral cover occur between 1-15 m depth. To be useful for coupling with coral reef
biological data, these temperature data must be relatively accurate beyond the 'skin' of the ocean. We used linear regression to examine how data from in situ reef temperature loggers compared with data from the CoRTAD to determine how accurate the temperature data were at a variety of depths and locations around the world (Table S1.1).

**Temperature anomaly metrics**

Several metrics could be used to link coral reef ecosystem health with temperature including trophic structure, diversity or percent coral cover (Roberts et al. 2002; Newman et al. 2006; Bruno & Selig 2007). However, we focused our analysis on coral bleaching and disease because they are key drivers of coral decline and their relationships with temperature are better understood (Glynn 1993; Aronson & Precht 2001; Bruno et al. 2007). Analyses were performed on two metrics (Table 1): one that is commonly known to lead to bleaching (Glynn 1993; Liu et al. 2003; Strong et al. 2004), and one that is correlated with increased disease severity (Selig et al. 2006; Bruno et al. 2007). Coral bleaching results when corals lose their symbiotic zooxanthellae (Glynn 1993, 1996). Bleaching is a natural stress response not only to warm temperatures, but also to cool temperatures (Hoegh-Guldberg & Fine 2004) as well as light and salinity values different from the normal range (Glynn 1993). Corals can recover from bleaching, but their ability to do so is dependent on the magnitude and duration of the anomaly event (Glynn 1993). The temperature thresholds that result in coral bleaching vary by location and species (Berkelmans & Willis 1999). Bleaching is often connected to Thermal Stress Anomalies (TSA), defined as occurring when temperatures exceed 1°C more than the climatologically warmest week of the year (Table 1, Glynn 1993). The temperature anomaly thresholds relevant to disease have been studied in only one
pathogen-host system (Selig et al. 2006; Bruno et al. 2007). In that system, changes in
disease cases were correlated with Weekly Sea Surface Temperature Anomalies (WSSTAs),
temperatures that were 1°C greater than the weekly average for that location.

The best metric for predicting bleaching or disease may vary according to location,
species, and pathogen (Berkelmans 2002; Selig et al. 2006; Bruno et al. 2007). For example,
bleaching on the Great Barrier Reef was best predicted by the maximum anomaly over a 3
day period (Berkelmans et al. 2004), rather than an anomaly metric like the TSA. Although
the 7-day averaging approach in the CoRTAD may be too temporally coarse to capture all
bleaching events, it is necessary to maintain consistency and minimize gaps in the dataset
across broad spatial scales. In addition, the data will be less likely to yield false positives for
TSAs and will likely capture most WSSTA events, which have a lower temperature
threshold.

**Anomaly frequency, temporal duration and magnitude**

We calculated both the frequency of TSAs and WSSTAs based on the number of
anomalies in each calendar year and cumulatively over the 21-year study. Anomaly
magnitude and duration, two important predictors of coral bleaching and disease, may also
play roles in the percent mortality during a thermal event (Glynn 1993; Winter et al. 1998;
Berkelmans et al. 2004). Anomaly magnitudes were calculated over the whole time series.
We quantified anomaly duration by each anomaly event, which we defined as beginning
when ocean temperatures exceeded the threshold value for TSA or WSSTA and ending when
temperatures returned below the threshold again. Only locations that had an anomaly and
were located on a reef were included in the analysis.
region delineations

We delineated regions within ocean basins to better understand how anomaly patterns varied at regional scales (Fig. 1.2). These regions vary in total area, but they represent general regions of similar diversity and biogeography (Roberts et al. 2002), major bathymetric breaks, or management. These demarcations are similar to marine ecoregions recently defined by several conservation organizations (Spalding et al. 2007). We restricted our analysis to regions that have substantial coral reef area and were large enough not to cause edge effects in the calculation of anomaly areas. Thus, we did not include reefs off the coasts of Brazil, West Africa, Bermuda and parts of southeastern and western Australia.

Coral reef location data

Shallow coral reef location data were compiled from a variety of freely available datasets. The initial GIS layer was developed from Reefs at Risk (Bryant et al. 1998) and Reefs at Risk in Southeast Asia (Burke et al. 2002), which used data from the United Nations Environment Program – World Conservation Monitoring Centre (UNEP-WCMC). These data were improved with additional data from scientists and governmental agencies. We then added GIS data from ReefBase and Reef Check to capture additional reef areas worldwide. Data included both polygons and points, which were then gridded at a resolution of 1 km (Fig. 1.2).

Calculation of anomaly areas

We calculated patterns in anomaly area for both WSSTAs and TSAs throughout the tropics. For each metric, we first created 1096 weekly grids of anomaly presence and
absence for all the weeks in the database. We only calculated areas for anomalies that contained at least one grid cell that overlapped a known coral reef location. We used the bwlabel function in the Image Processing Toolbox in Matlab 7.3 (The Mathworks Inc. 2006) to identify each anomaly and determine whether it was connected to a neighboring thermal event in any of the eight adjacent grid cells.

Results

CoRTAD Validation

Although the AVHRR sensor theoretically measures only the 'skin' of the ocean, the Pathfinder processing attempts to create a 'bulk' sea surface temperature more representative of the temperature at approximately 1 m depth. In fact, we found that the temperature data in the CoRTAD were quite accurate over a wide range of coral locations and depths down to at least 10 m. The CoRTAD typically had $r^2 > 0.90$ when compared with in situ temperature loggers for most of the studied coral reef areas (Table S1.1). Accuracy will clearly depend on local oceanographic conditions, particularly the degree of stratification and depth. Because the AVHRR instruments are affected by atmospheric absorption of surface IR radiance, temperature measurements can be less accurate as a result of cloud cover (water vapor), aerosols, vapor, CO$_2$, CH$_4$, and NO$_2$ (Kilpatrick et al. 2001). Validations based on only a few satellite and in situ match up points (<50) may yield artificially lower correlations (Table S1.1).
Anomaly frequency

Anomaly frequencies varied by year and by region (Figs. 1.3-4) for both WSSTA (disease) and TSA (bleaching) metrics. Spatial patterns for the two metrics were very similar. Because the temperature threshold for attaining a TSA is higher, the number of TSAs was almost always lower than the number of WSSTAs. Over the 21-year period analyzed, TSA frequency varied from a cumulative average of 13 events in the Florida Keys to an average of 87 events in the Central Pacific (Figs. 1.3A-B). At the reef scale, the average TSA frequency across 21 years was 37 anomalies and the maximum was 444 anomalies. In a typical year, there were an average 1-4 TSAs and 4-11 WSSTAs (Figs. 1.5A-B) on a given reef. However, frequencies changed drastically for some regions during major events, such as El Niño.

We also examined patterns in anomaly frequencies by year to provide insight into whether more recent years had more TSAs than earlier years in the database (Figs. 1.6-7). In the Caribbean, the Mesoamerican Barrier Reef, Gulf of Mexico, and Eastern Caribbean regions all had the highest number of anomalies in 1998 (Figs. 1.2, 1.6). There were also a significant number of anomalies in 2005, particularly in the Antilles region (Figs. 1.2, 1.6). In the Pacific, the signature for the 1998 El Niño event was very clear, particularly in the Central Pacific, but the Indo-Pacific still had areas that did not have their maximum frequency in that year. For example, much of the territorial waters of Indonesia between Kalimantan and West Papua experienced greater anomaly frequencies during the 1987-1988 El Niño event (Fig. 1.7). Nonetheless, the severity of the 1998 El Niño in the Indo-Pacific and the 2005 event in the Caribbean was clear both in the number of bleaching-related
anomalies and in the ratio of anomalies in those years compared with other years (Figs. 1.8-9).

Anomaly durations

The duration of temperature anomalies has long been known to affect bleaching events (Glynn et al. 1988), although its effect on coral disease severity remains poorly understood. Mean TSA durations varied considerably by region (Fig. 1.5C). The Central America, Persian Gulf, and Pacific Central America regions had the longest mean anomaly durations, averaging approximately 1.8 weeks (Figs. 1.5C, S1.1, and S1.2). During the 1998 El Niño event, TSA anomaly durations were markedly higher in Pacific Central America, South China Sea, and the Persian Gulf, where durations averaged 6, 3.1 and 4.4 weeks, respectively (Fig. S1.3; Persian Gulf not shown). Although anomaly durations were higher for other regions during El Niño years, they were within the standard deviation of the long-term averages (Graham et al. 2006). Anomaly durations for WSSTAs were longer, particularly in Pacific Central America and Taiwan and Japan, where they averaged more than 2 weeks (Fig. 1.5D). Like TSAs, WSSTA durations were greater during El Niño events in nearly every region except those in the Caribbean (Fig. S1.4).

Anomaly magnitudes

Absolute anomaly magnitudes between WSSTAs and TSAs were not directly comparable because of the different temperature thresholds. Anomaly magnitudes were highest for the Red Sea and Persian Gulf regions. Typical mean TSA magnitudes over the whole time series varied between 1.4°C in the Western Pacific to 1.8°C in the Persian Gulf (Fig. 1.5E).
WSSTAs displayed a similar overall pattern to TSAs. Over the whole time series mean magnitudes of WSSTAs ranged from 1.3°C in the Western Pacific to 1.8°C in the Persian Gulf (Fig. 1.5F).

Anomaly areas
Anomaly areas displayed relatively similar patterns for WSSTAs and TSAs (Fig. 1.10) with most anomalies having small areas and a large number of occurrences. Spatially very large anomalies (<500 km²) occurred, but represented less than 10% of the data. There was a marked difference between TSAs and WSSTAs in the total number of events, although this probably results from the higher temperature threshold required to be counted as a TSA. From 1985-2005, there were 398,931 TSAs and 1,000,525 WSSTAs. However, both metrics had relatively the same percentage of anomalies in different area categories. For example, 33% of TSAs and 29% of WSSTAs were between 1-25 km² in size, the smallest size category, which corresponds roughly to one grid cell. More than 90% of TSAs and WSSTAs were 1-425 km² and 1-500 km², respectively.

Discussion
The frequency, magnitude, and extent of temperature anomalies can be used to quantify disturbance severity and its role in the regulation of ecological communities (Connell 1978; Menge & Sutherland 1987). We found substantial variability in the frequency, duration, and magnitude of the temperature anomalies that can lead to bleaching and disease both within and across regions and across years. Anomalies were highly
pervasive even in non-extreme years, but nearly 50% of the anomalies that can cause bleaching were less than 50 km². Overall, these results suggest that although temperature anomalies are spatially extensive, their fine-scale spatial structure will result in highly localized effects on coral disease and bleaching.

Patterns in anomaly frequency, magnitude, and temporal duration affect the occurrence and severity of bleaching and disease events, although several other physical (e.g., light) and biological (e.g., coral cover) parameters may be necessary or synergistic factors (Glynn 1993; Bruno et al. 2007). Frequencies for both bleaching- and disease-related anomalies were highly regionally-specific and strongly correlated with large-scale climatic patterns like El Niño events (Figs. 1.3-4). Temperature anomalies are known to exhibit high spatial heterogeneity on reefs according to depth, site, and season (Leichter et al. 2006). This heterogeneity was common across reefs globally, although regional patterns and differences between bleaching and disease-related anomalies also emerged (Fig. 1.5A-F). The highest mean TSA frequencies in the Caribbean were found in the Central America region whereas the Florida Keys experienced the highest WSSTA frequencies. Differences in the characteristics of TSAs and WSSTAs could be indicative of greater regional vulnerability to bleaching or disease. Although the presence of an anomaly connotes conditions that may be favorable to the development of bleaching or disease, they are not necessarily predictive of actual changes in coral condition. Nonetheless, these regional patterns describe baseline characteristics to which future changes in anomalies or coral condition can be compared.

Our results also provided spatial context for how severe the 1998 El Niño and the 2005 warm event in the Caribbean were compared to major thermal events during 1985-2005. The severe 1998 El Niño event in the Indo-Pacific (Fig. 1.8) was clearly
unprecedented in the last 20 years, as was the 2005 warm event in the eastern Caribbean (Fig. 1.9). Yet even during these extreme events, substantial local and regional variability existed (Figs. 1.6-7). Although 33% of reefs in the Caribbean had their 21-year peak in number of anomalies during 2005, 18% of reefs had the highest number of anomalies during 1998 (Fig. 1.6). Similarly, during the 1998 El Niño, 21% of reefs in the Indo-Pacific experienced the highest recorded anomaly frequencies. Yet, across much of eastern Indonesia and the Great Barrier Reef, frequencies were higher during the 1988 and 2002 El Niño events (Fig. 1.7). Throughout the Indo-Pacific, 10% of reefs had their highest anomaly frequencies during 2002. Indeed, although the Great Barrier Reef experienced extensive bleaching in 1998, the most severe and extensive bleaching on record occurred in 2002 (Berkelmans et al. 2004).

These results suggest that anomalies are spatially ephemeral in nature and may have different patterns even when associated with large climatic patterns like El Niños, which have well-established spatial signatures.

We also found that the total spatial extent of anomalies was extensive, but there was substantial fine-scale spatial structure. From 1985 to 2005, all coral reef locations within our study regions experienced at least one anomaly. Even in individual years, a considerable percentage of reefs had at least one anomaly. During 1985, a non-extreme year, the Great Barrier Reef had at least one bleaching-related anomaly in over 67% of the total area in the region. In comparison, during the 1998 El Nino event, 84% of the Great Barrier Reef was affected. In spite of the large area anomalies can affect, globally the anomalies themselves were typically small in size. Over 21 years, 48% of bleaching anomalies and 44% of disease anomalies were less than 50 km², smaller than the spatial resolution of many climate models and temperature anomaly datasets (Fig. 1.10). Therefore, even though a substantial portion
of total reef area may be affected during a thermal event, bleaching-related coral losses may be spatially patchy.

Coral bleaching and disease can have dramatic effects on the abundance and composition of corals and coral reef ecosystem health (Aronson et al. 2002; Graham et al. 2006; Ledlie et al. 2007). During major thermal events like the 1998 El Niño, more than 50% of live coral cover in affected sites can be lost (Sheppard 1999; Aronson et al. 2000; Bruno et al. 2001). Although the dynamics of temperature anomalies and loss of coral cover through disease outbreaks are less well understood, several coral diseases are associated with elevated temperatures (Kuta & Richardson 2002; Patterson et al. 2002; Bruno et al. 2007). Declines in coral cover through disease and bleaching can have drastic effects on the entire coral reef ecosystem (Aronson & Precht 2001; Jones et al. 2004; Graham et al. 2006). Studies of individual reefs that have undergone coral mortality from the 1998 El Niño event have found subsequent parallel declines in fish abundance and diversity (Jones et al. 2004) and erosion of the reef framework itself (Graham et al. 2006) even on protected and isolated reefs. Decreased shoreline protection from storms and declines in fisheries from loss of the reef structure potentially jeopardize US$129-$375 billion/year in value from coral reef ecosystem services (Costanza et al. 1997).

The dramatic decline in coral reefs have made monitoring and predicting vulnerability to coral reef bleaching and disease key priorities for scientists, conservationists, and policymakers. Our results characterize the frequency, magnitude, and extent of bleaching and disease-related temperature anomalies and their natural variability. These data can be used for a variety of applications to better understand how climate change is affecting the temperature anomalies causing coral reef decline. Time series analyses of specific areas
may help elucidate whether the frequency, magnitude, and duration of anomalies are increasing over time. In addition, these data can be used to generate spatial maps of anomaly durations and magnitudes to get a picture of what the typical patterns would be for specific locations. Managers can then determine how unusual future events are for their areas. If paired with in situ observations of coral cover, bleaching, and disease, these data could also be used to develop local and regional portraits of vulnerability to temperature stress.

Understanding the scale of variability in temperature anomalies is a critical step towards characterizing ocean temperature patterns and their relationship to ecosystem response. Even minor changes in the local dynamics of physical factors like temperature can have dramatic effects on ecosystems. Models in the Caribbean predict that rises of only 0.1°C in regional ocean temperatures could trigger 35% and 42% increases in the geographic extent and intensity of coral bleaching, respectively (McWilliams et al. 2005). However, documenting these patterns alone clearly will not be enough to predict ecosystem response to climate change. Local conditions could be affected by management interventions, the synergistic effects of other stressors, and species composition (Harley et al. 2006). Our results highlight the importance of incorporating finer scale data into climate models so that we can more accurately assess vulnerability to temperature changes and design relevant management interventions.
Figure 1.1 Comparison of the 4 km Pathfinder with other satellite datasets. An example of the benefits of increasing resolution on the Great Barrier Reef from; (A) 50 km HotSpot data to (B) 9 km Pathfinder data to (C) 4 km Pathfinder data. In the 4 km data, there is less missing data, allowing for greater coverage of coastal areas where many reefs occur. In addition, the 4 km data displays more spatial structure and precision in the temperature values. Data are from January climatological averages, monthly for the 50 km and from the first week of January for the 9 km and 4 km data.
Figure 1.2 Region delineations for the CoRTAD analysis. (GBR = Great Barrier Reef, MBR = Mesoamerican Barrier Reef, and SCS = South China Sea). Purple dots are locations of coral reefs.
Figure 1.3 Cumulative number of TSAs (1985-2005) in (A) Indo-Pacific and (B) Caribbean.
Figure 1.4 Cumulative number of WSSTAs (1985-2005) in (A) Indo-Pacific and (B) Caribbean.
Figure 1.5 Mean frequency, duration, and magnitude of TSAs and WSSTAs.

Temporal average of mean TSA (A) and WSSTA (B) frequency and 95% confidence intervals (bars) from 1985-2005 for the studied regions (see Figure 2). Mean duration for TSA (C) and WSSTA (D) as well as mean magnitude for TSA (E) and WSSTA (F) are also shown. In each panel, the data are ordered by ocean basin: Caribbean Sea (top), Indian Ocean (middle), and Pacific (bottom) and sorted regionally from highest to lowest mean value.
E

F

Arctics
E. Caribbean
Bahamas
C. America
Mesosamerican BR
Florida Keys
Red Sea
Persian Gulf
SE Africa
E. Indian Ocean
Andaman / Nicobar Is.
Pacific C. America
Hawaiian Islands
Central Pacific
South China Sea
Philippines
Taiwan and Japan
East Indonesia / PNG
GBR
W. Indonesia
SW Pacific
SE Pacific
Western Pacific

Mean TSA magnitude (°C)

Mean WSSTA magnitude (°C)
Figure 1.6 Year of the maximum number of TSAs in the Caribbean. For each grid cell, the year with the greatest number of TSAs was recorded. The signature of the 2005 warm event is clearly visible in the Antilles region.
Figure 1.7 Year of maximum number of TSAs in the Pacific. For each grid cell, the year with the greatest number of TSAs was recorded. Although most locations had their maximum TSAs during the 1998 El Niño event (yellow), several other El Niño years including 1988 (light blue) and 2002 are also visible.
Figure 1.8  Severity of the 1998 El Niño event. (A) The number of TSAs in 1998 and (B) the ratio of the number of TSAs in 1998 relative to the number of TSAs from 1985-2005. The 1998 El Niño event was unusual for equatorial Pacific and much of the Indian Ocean.
Figure 1.9 Severity of the 2005 warm event. (A) The number of TSAs in 2005 and (B) the ratio of the number of TSAs in 2005 relative to the number of TSAs from 1985-2005. The warm event in the Antilles region produced anomaly frequencies unprecedented in the last 21 years.
Figure 1.10  Frequency distribution of anomaly areas for TSAs and WSSTAs for 1985-2005. TSAs are shown with the solid black line and WSSTAs with the dashed grey line. Most climate studies occur at a spatial resolution of 50 km² (dotted grey line). Raw anomaly areas were categorized into 25 km² bins.
Table 1.1 Metrics of thermal stress.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Question</th>
<th>Application</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thermal stress anomalies (TSA)</td>
<td>Is the temperature ≥1°C warmer than typical summertime highs?</td>
<td>Bleaching</td>
<td>(Glynn 1993; Podesta &amp; Glynn 2001; Liu et al. 2003)</td>
</tr>
<tr>
<td>Weekly sea surface temperature anomalies (WSSTA)</td>
<td>Is the temperature ≥1°C warmer than usual for that week of the year?</td>
<td>Disease</td>
<td>(Selig et al. 2006; Bruno et al. 2007)</td>
</tr>
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Acknowledgements

For temperature data: Erich Bartels of MOTE Marine Laboratory and Peter Edmunds of California State University-Northridge; T. Kristiansen and M. O'Connor for comments on the manuscript.
References


CHAPTER 2

Analyzing the relationship between ocean temperature anomalies and
coral disease outbreaks at broad spatial scales

Abstract

Ocean warming due to climate change could increase the frequency and severity of infectious
coral disease outbreaks by increasing pathogen virulence or host susceptibility. However,
little is known about how temperature anomalies may affect disease severity over broad
spatial scales. We hypothesized that the frequency of warm temperature anomalies increased
the frequency of white syndrome, a common scleractinian disease in the Indo-Pacific. We
created a novel 4 km satellite temperature anomaly dataset using data from NOAA’s
Pathfinder program and developed four different temperature anomaly metrics, which we
correlated with white syndrome frequency at 47 reefs spread across 1500 km of the Great
Barrier Reef. This cross-sectional epidemiological analysis used data from disease field
surveys conducted by the Australian Institute of Marine Science six to twelve months after
the summer of 2002, a year of extensive coral bleaching. We found a highly significant
positive relationship between the frequency of warm temperature anomalies and the
frequency of white syndrome. There was also a highly significant, nearly exponential
relationship between total coral cover and the number of disease cases. Further, coral cover
modified the effect of temperature on disease frequency. Both high coral cover ( > 50%) and
anomalously warm water appear to be necessary for white syndrome outbreaks to occur and these two risk factors explained nearly 75% of the variance in disease cases. These results suggest that rising ocean temperatures could exacerbate the effects of infectious diseases on coral reef ecosystems.

Introduction

Over the last four decades, coral cover has declined dramatically on reefs worldwide (Gardner et al. 2003; Bellwood et al. 2004). Several factors are thought to be responsible for this decline including overfishing (Jackson 1997; Pandolfi et al. 2003), terrestrial run-off (Fabricius 2005), climate change (Hoegh-Guldberg 1999; Hughes et al. 2003), and infectious disease (Aronson & Precht 2001). There is growing recognition that we need to focus on possible synergisms among these and other stressors (Hughes & Connell 1999; Lenihan et al. 1999). In the last several years, the relationship between climate conditions and disease has received more attention as researchers have connected factors such as temperature and precipitation with increases in human and wildlife diseases (Pascual et al. 2000; Patz 2002; Kutz et al. 2005; Pounds et al. 2006). Yet, few studies have focused on the effects of climate change on diseases in the ocean, particularly at broad spatial scales.

Disease has already had significant effects on coral reef ecosystems. Several diseases have altered the landscape of Caribbean reefs, causing the near extirpation of the keystone herbivore Diadema antillarum (Lessios 1988) and dramatic losses of Acropora cervicornis and Acropora palmata (Aronson & Precht 2001; Aronson et al. 2002). These disease outbreaks mediated a shift from coral- to algal-dominated communities in the Caribbean.
(Aronson & Precht 2001). The scale and severity of coral loss on many Caribbean reefs is unprecedented in the paleontological record (Aronson & Precht 2001; Wapnick et al. 2004) of many reefs and indicative of the emergence of a novel stressor (Aronson & Precht 2001). Recent studies quantifying both disease reports (Ward & Lafferty 2004) and the number of described coral diseases (Sutherland et al. 2004) suggest that the frequency of marine diseases is increasing and many of these diseases are the result of previously unknown pathogens. Reports from the Pacific indicate that diseases of reef-building corals may be far more widespread than previously believed (Sutherland et al. 2004; Willis et al. 2004; Aeby 2005; Raymundo et al. 2005). Although coral disease is likely underreported in the Pacific due to a lack of disease research, increases in coral disease cases have been detected since the late 1990s (Willis et al. 2004). These lines of evidence provide strong support for the hypothesis that there has been a real increase in the number of coral disease reports over the last three decades (Harvell et al. 1999; Ward & Lafferty 2004).

The causes underlying recent increases in coral disease outbreaks are complex and poorly understood, in part because of a paucity of knowledge about the identity and sources of most coral pathogens (Sutherland et al. 2004). Pathogens have a variety of purported vectors and reservoirs including algae (Nugues et al. 2004), invertebrates (Rosenberg & Falkovitz 2004; Williams & Miller 2005), sediment transported from the Sahel region of northern Africa (Shinn et al. 2000), and sewage effluent (Patterson et al. 2002). In addition, some diseases are hypothesized to be associated with changes in corals’ microbial communities, rather than the result of an external infectious pathogen.

Abiotic factors like nutrients and temperature can exacerbate disease severity, but the scale of their effects may vary. For example, nutrients increased the severity of two coral
diseases in experimental manipulations (Bruno et al. 2003). However, inputs of terrestrial pollution, including nutrients, do not always result in elevated disease levels on affected reefs (Weil 2004; Willis et al. 2004). Although localized inputs of nutrients may play some role in disease outbreaks, the regional scale of most outbreaks (Aronson & Precht 2001; Kim & Harvell 2004) indicates that a climatic variable like temperature may be a critical driver of disease dynamics. For example, disease prevalence, or the proportion of the total population that is diseased, may be related to the frequency and magnitude of warm temperature anomalies. Extensive work clearly links these anomalies to coral bleaching events (Glynn et al. 1988; Glynn & D'croz 1990; Hoegh-Guldberg 1999; Bruno et al. 2001; Fitt et al. 2001; Liu et al. 2003; Strong et al. 2004). Since bleaching is a sign of physiological stress in corals (Glynn 1993; Brown 1997), it is expected that bleached or thermally-stressed corals would be more susceptible to opportunistic and residential pathogens (Hayes et al. 2001; Rosenberg & Ben-Haim 2002).

Forecast sea surface temperature (SST) models predict that the frequency and severity of warm temperature anomalies will increase with climate change (Hoegh-Guldberg 1999; Sheppard 2003; Sheppard & Rioja-Nieto 2005). Ocean temperature has already increased, on average, 0.4-0.8°C (Folland et al. 2001) from 1861 to 2000, with some regional variation (Casey & Cornillon 2001). These anomalies and the general warming of the ocean could have several effects on disease. One possible outcome of global warming is that the summer “disease season” may become more severe, as summer temperature maxima increase, and longer, as these elevated thermal regimes start earlier and persist later in the season. Seasonal variability in coral disease abundance has been found in multiple field studies in different regions. In the Caribbean, several coral diseases, including black band (Edmunds
white pox (Patterson et al. 2002), and dark spots disease (Gil-Agudelo & Garzon-Ferreira 2001), are more prevalent or spread across colonies more rapidly during summertime than during cooler seasons. On the Great Barrier Reef (GBR), white syndrome frequency was greater in summer than winter on surveyed reefs (Willis et al. 2004). Similarly, in the summer of 2002 on the GBR, Jones et al. (2004) documented a localized outbreak of atrementous necrosis. In addition, shorter or warmer winters may release some infectious diseases from the low temperature control that provides hosts with a seasonal escape from disease (Harvell et al. 2002). Climate warming has also been predicted to alter the geographic distributions of infectious diseases by shifting host and pathogen latitudinal ranges pole-ward (Marcogliese 2001; Harvell et al. 2002).

Testing the hypothesis that the frequency or intensity of temperature anomalies can influence coral disease dynamics requires high quality data on temperature and disease frequency. Here we discuss how analyses of these broad scale questions are now possible using a newly developed high-resolution satellite temperature anomaly dataset. We then present a case study where we examine the effects of the warm temperature anomalies on white syndrome, an emergent sign of disease on GBR corals. We also discuss future research directions for testing the relationship between temperature and disease.

Using remote sensing data to explore the climate warming disease outbreak hypothesis

Most documented coral disease outbreaks have been at the scale of ocean basins (Lessios 1988; Aronson & Precht 2001; Willis et al. 2004). Previously, correlating these outbreaks with ocean temperature was complicated by a scale mismatch. Temperature has
typically been measured with relatively high accuracy at very fine scales or with less accuracy at coarse scales. *In situ* temperature loggers can be highly effective at capturing small-scale variability (1-100 m) (Leichter & Miller 1999; Castillo & Helmuth 2005; Leichter *et al.* 2005), but are limited in their spatial extent. On the other hand, the 50 km HotSpot mapping (Fig. 2.1) (Strong *et al.* 2004), although effective for predicting bleaching at broad scales (Bruno *et al.* 2001; Berkelmans *et al.* 2004; Strong *et al.* 2004), is too coarse to accurately represent the temperature of waters surrounding many reefs and may not sufficiently capture local variability (Toscano *et al.* 2000). Therefore, the development of new, higher resolution remote sensing products is required to detect correlations between temperature anomalies and disease outbreaks.

We developed a novel satellite temperature anomaly product to investigate the relationship between sea surface temperature and disease at broad spatial scales. Our dataset used the 4 km Advanced Very High Resolution Radiometer (AVHRR) Pathfinder Version 5.0 SST dataset produced by NOAA’s National Oceanographic Data Center and the University of Miami’s Rosenstiel School of Marine and Atmospheric Science (http://pathfinder.nodc.noaa.gov). These data now provide the longest sea surface temperature record at the highest resolution of any global satellite dataset. The Pathfinder Version 4.2 dataset had a 9 km resolution (Kilpatrick *et al.* 2001), a marked improvement from the 50 km data. However, inaccuracies in the land mask, which defines the extent of the data, resulted in coverage of only 60% of reef areas (Fig. 2.1). Using a more refined climatology and more accurate coefficients for generating temperatures, the 4 km Pathfinder Version 5.0 dataset reprocessed the full AVHRR record from 1985 through 2005 to remove inaccuracies. With these improvements, temperature records are now available for more than
98% of reefs worldwide. Appropriate use of satellite temperature data requires validation with *in situ* loggers (Reynolds *et al.* 2002). In theory, an infrared observing satellite like AVHRR only measures an integrated temperature over approximately the top 10 micrometers of the ocean surface. Therefore, we validated the assumption that the 4 km Pathfinder Version 5.0 SST values reflect temperatures on shallow reefs, where the majority of reef-building corals are found, by comparing satellite temperature estimates to *in situ* temperature logger data collected by the Australian Institute of Marine Science (www.reeffutures.org) on nine shallow reefs on the GBR (5 m to 9 m depth). We fit a linear multilevel model and found a highly significant relationship (*p* < 0.0001) with a common value for the slope of all the reefs of 0.96 (SE = 0.017). We found the difference between satellite-derived and benthic temperatures was generally less than the 0.2°C error of most *in situ* loggers. We also ran linear regression analyses for each reef to investigate the generality of this relationship at all nine reefs (Table 2.1) and found that the satellite temperature measurements were a very good predictor of benthic water temperature.

One key advantage of satellite data is their ability to provide a long-term temporal record of temperature values, which enables users to create accurate climatologies, or average long-term patterns (Fig. 2.2). These climatologies are then used as the basis for calculating deviations from typical weekly, monthly, seasonal, or annual temperatures. For disease analyses, relevant data include the frequency of deviations or temperature anomalies, the duration of anomaly events, occurrence of wintertime anomalies, and the geographic extent of the anomaly.
Case study on the Great Barrier Reef

The Great Barrier Reef (GBR) is the largest barrier reef system in the world and one of the most highly managed, with more than a third of reef area in marine reserves, or no-take areas (Fernandes et al. 2005). Recent surveys suggest that disease is more prevalent than previously believed on the GBR (Willis et al. 2004). Black band, white syndrome, brown band, and skeletal eroding band have all been reported on the GBR (Willis et al. 2004). In spite of the well-documented relationship with increased temperatures and black band disease in the Caribbean (Edmunds 1991; Kuta & Richardson 2002), it did not vary in frequency over the course of our study (Willis et al. 2004). Instead we focused our analysis on white syndrome, which increased dramatically in 2002-2003 on some reefs. We tested specific hypotheses about how temperature might affect disease frequency by using an information-theoretic approach to evaluate different thermal stress metrics.

Disease surveys

The disease data used for this analysis were collected by the Australian Institute of Marine Science’s Long-term Monitoring Program (AIMS LTMP) during their 2002-2003 surveys. Surveys were performed at 47 reefs in a stratified design. Five permanent 50 m x 2 m belt transects were surveyed at three sites on each reef at approximately 6-9 m depth (Full methods in Sweatman et al. 2003). For each transect, the number of colonies infected with white syndrome was quantified. Reefs were grouped by latitudinal sectors, which together cover more than 1500 km and a variety of different oceanographic regimes (Fig. 2.3). White syndrome is characterized by a band of recently-exposed white skeleton, sometimes preceded by a band of bleached tissue at the tissue-skeleton interface. The white band moves across
the colony as the front of tissue mortality progresses, potentially resulting in mortality of the whole colony (Fig. 2.4). White syndrome has been recorded on at least 17 species from 4 families including Acroporidae, Pocilloporidae and Faviidae, which together constitute a significant percentage of overall coral cover on the GBR (Willis et al. 2004). White syndrome is similar to Caribbean white diseases such as white band I, white band II, white plague I, and white plague II in its disease signs. Because the pathogen(s) that cause white disease in the Pacific are not known, we cannot state with certainty that the syndrome does not represent more than one distinct disease (Willis et al. 2004) or that the underlying etiology is infectious.

**Temperature data**

Consistent with previous analyses of satellite data in coral studies, we used nighttime weekly temperature averages (Liu et al. 2003; Strong et al. 2004). Nighttime daily averaged data had too many gaps and would have required extensive interpolation. Although they may not capture short duration events, weekly data provide substantially more continuity in the record and still represent a time scale short enough to capture most thermal stress events that negatively impact corals (Glynn 1993; Podesta & Glynn 2001). To measure anomalies, we first calculated weekly climatologies, or the mean values at each calendar week from 1985-2004 for each 4 x 4 km pixel (Fig. 2.2). Missing data in the climatologies were interpolated using a Piecewise Cubic Hermite Interpolating Polynomial (PCHIP) function in MATLAB (The Mathworks Inc. 2005). The climatologies were then smoothed using a five-week running mean to minimize unusual fluctuations from periods of limited data availability.
Gaps in weekly temperature observations were also interpolated using the PCHIP function without modifying the original data.

**Thermal stress metrics**

To test the hypothesis that temperature affects disease frequency, we first designed temperature metrics relevant to disease. Infectious diseases are interactions between hosts and pathogens. Temperature can increase host susceptibility, but it can also increase pathogen growth rate, transmission rate, and over-wintering survival (Harvell *et al.* 2002). Because of the potential complexity of this relationship and the paucity of data about most pathogens, no specific algorithm exists for disease prediction. However, data on how corals respond to stress and epidemiological theory provide a general guide to temperature thresholds that may be applicable to disease dynamics. We developed a series of temperature metrics for our case study based on metrics known to have a physiological effect on coral health. Three of our four thermal stress metrics are based on an anomaly threshold of 1°C, because this is widely assumed to estimate the point at which a warm temperature anomaly induces a measurable physiological stress in a coral host, (Glynn 1993; Winter *et al.* 1998; Hoegh-Guldberg 1999; Berkelmans 2002) and in general, increases of ≥1°C above normal summertime temperatures are thought to induce bleaching (Glynn 1993, 1996; Winter *et al.* 1998; Hoegh-Guldberg 1999; Berkelmans 2002). All of the metrics measured deviations from the location-specific climatologies we created. Because disease surveys were conducted at different times of year (November-March), we standardized all of our metrics to include the number of anomalies during the 52 weeks prior to each disease survey. We then
used the latitude and longitude of each reef to match it with its corresponding pixel in the satellite data.

We developed each temperature metric to investigate a specific hypothesis related to the relationship between thermal stress and disease. The first three metrics are location-specific and assume that corals are acclimated to the thermal regime at their location. Work by Berkelmans and Willis (1999) suggests that corals exhibit some degree of local acclimation or adaptation. The fourth metric assumes that temperature is affecting disease rates at regional scales. If thermal anomalies are acting on the pathogen itself, by increasing growth or reproductive rates, they would likely be acting at a regional scale due to high pathogen mobility (McCallum et al. 2003).

**Metric descriptions**

1) *WSSTA = Weekly Sea Surface Temperature Anomalies* = deviations of 1°C or greater from the mean climatology during a particular week at a given location from 1985-2003. This metric is designed to be both location and season-specific by determining whether the temperature is unusual for that location at a particular week of the year.

2) *TSA= Thermal Stress Anomalies* = deviations of 1°C or greater from the mean maximum climatological weekly temperature from 1985-2003. The mean maximum climatological week is the warmest week of the 52 weekly climatologies. This metric is also site-specific but designed to detect deviations from typical summertime highs and is similar to metrics used by the Coral Reef Watch program (Liu et al. 2003; Strong et al. 2004).
3) \( LTSA = \text{Local Temperature Stress Anomalies} = \) deviations from the upper 2.5\% of all weekly measurements taken at that location from 1985-2003. This metric is site-specific. It is designed to detect whether temperatures are unusual based on the distribution and extremes of all measured temperatures, regardless of calendar week.

4) \( RTSA = \text{Regional Thermal Stress Anomalies} = \) deviations from the upper 2.5\% of all weekly measurements taken at all reefs. For this metric, local temperatures are compared to regional average values.

**Metric selection and statistical analysis**

We evaluated the different thermal stress metrics (Table 2.2) using Akaike Information Criterion (AIC) (Akaike 1973). Identifying which thermal stress metric best explains the relationship between temperature and disease can facilitate the development of an appropriate model for a specific coral-pathogen system. Different diseases may be affected by different temperature characteristics. For example, TSAs may be highly correlated with an increase of one disease while another disease may be more correlated with WSSTAs. AIC is an estimate of expected relative Kullback-Leibler information, an information-theoretic measure of the distance between models where smaller AIC values should be preferred. In practice, only the relative differences in AIC between models are meaningful. When these differences are normalized as Akaike weights, \( w_i \), they can also be given a probabilistic interpretation. Each \( w_i \) is the weight of evidence favoring model \( i \) as the best model among the models under consideration (Anderson et al. 2000; Anderson & Burnham 2002).
Coral cover is clearly related to the number of white syndrome cases on a reef (Fig. 2.5A) and was also included in the analysis. We used multiple, nonlinear regression analysis (StataCorp LP 2006) to analyze the relationship between the two independent variables, thermal stress and coral cover, and the dependent variable, the total number of white syndrome cases at each reef (i.e., the number/1500m²). We used a Poisson model and a quadratic function for the thermal stress metrics and a linear function for coral cover.

**Results**

The austral summer in 2002 triggered the most extensive bleaching event ever documented on the GBR (Berkelmans *et al.* 2004). Surveys conducted after this summer found a major increase in disease frequency with some sampled reef areas having more than 300 cases of disease (Willis *et al.* 2004). AICₜ, a small-sample (second order) bias-adjusted variant of AIC (Burnham & Anderson 2002), indicated that the number of WSSTAs provided the best model fit (Table 2.2) and was used in the main analysis as the thermal stress metric. The whole Poisson regression model ($r^2 = 0.73$) and both main effects (WSSTAs and coral cover) were all highly statistically significant at the reef scale (all $P < 0.0001$, n = 47). There was also a highly significant interaction between coral cover and WSSTAs ($P < 0.0001$). At low and intermediate cover (0-40%), the number of white syndrome cases was greatest when annual WSSTAs were 4-6 and declined slightly with increasing WSSTA (Fig. 2.6). However, when cover was high (> 41%), white syndrome frequency was more than 3 times greater when the frequency of WSSTAs was > 7 than when it was 4-6 (Fig. 2.6).
Discussion

Temperature anomalies are known to be the underlying cause of mass coral bleaching (Podesta & Glynn 2001; Liu et al. 2003; Berkelmans et al. 2004; Strong et al. 2004), but their relationship with infectious disease dynamics is not well understood. Our results suggest that warm temperature anomalies can significantly affect the frequency of white syndrome on the GBR, especially where coral cover is high. Total coral cover was clearly related to the number of white syndrome cases on a reef (Fig. 2.5A) (Willis et al. 2004). With few exceptions, white syndrome frequency was relatively low (< 30 cases/1500 m², the area surveyed at each reef) when coral cover was < 50% (Fig. 2.5A) and was very high, 192 cases ± 46 (mean ± 1 SE) at the eight reefs where coral cover was > 50%. The nearly exponential relationship between coral cover and disease cases (Fig. 2.5A) suggests there is a threshold coral cover of approximately 50% that is generally required to for an outbreak of white syndrome to occur. This could be due to higher host densities on high coral cover reefs. Host density is widely known to influence disease dynamics (Anderson & May 1986). White syndrome has been documented in the major coral families on the GBR, including the abundant staghorn and tabular species of Acropora (Willis et al. 2004). Therefore, total coral cover is likely to be directly related to white syndrome host cover. However, the relationship between host density and prevalence is not always clear for infectious coral diseases such as sea fan aspergillosis (Kim & Harvell 2004) possibly because secondary transmission is rare among host colonies (Edmunds 1991). Additionally, several other aspects of total coral cover could also influence the dynamics of white syndrome and other infectious coral diseases. For example, coral cover could be positively related to animal vectors (i.e. coral predators and mutualists), which could increase rates secondary transmission, although Willis
et al. (2004) found that the density of the corallivorous snail Drupella spp. was unrelated to white syndrome frequency on the GBR.

Temperature measured as WSSTA frequency also had a strong effect on the number of disease cases (Fig. 2.5B). The selection of the WSSTA metric as the best model using an AIC approach suggests that the effect of thermal stress on white syndrome is both season- and location-specific. The WSSTA metric is the only metric we tested that incorporates temperature anomalies throughout the year. These findings are consistent with coral physiology studies, which have found that at the beginning of cooler months, zooxanthellae densities increase and coral tissue is built up (Brown et al. 1999). With warmer or longer than usual summers or warmer winters these accumulations may not occur, increasing corals’ vulnerability to future stress (Fitt et al. 2001). Higher WSSTA frequencies may lead to chronic stress, which could increase host susceptibility and disease prevalence. However, WSSTAs could also have influenced disease frequency by increasing pathogen virulence. The relationship between WSSTA and white syndrome cases (Fig. 2.5B) is also suggestive of a weak threshold response when the number of annual WSSTAs exceeds approximately seven. There were several reefs with > 7 WSSTAs and a low number of cases (< 10), however, all were low coral cover reefs (mean cover 15.1 ± 3.0, n = 7). In fact, the only reefs with > 200 cases had > 50% cover and a WSSTA frequency > 7 (Fig. 2.5B), suggesting that both conditions are necessary for white syndrome outbreaks to occur. Furthermore, these two risk factors explained nearly 75% of the variance in disease cases.

White syndrome frequency varied substantially among the six sectors, possibly due in part to regional temperature variation. Average WSSTA frequency within sectors was positively related to average disease frequency, largely because Capricorn Bunkers, the
sector with by far the greatest number of cases also had the greatest number of WSSTAs (Fig. 2.7) and the highest average coral cover (Willis et al. 2004). Although other studies have found that higher nutrient levels are associated with increased disease severity (Kuta & Richardson 2002; Bruno et al. 2003), Willis et al. (2004) found that outer shelf reefs had higher levels of white syndrome than inner shelf reefs. Assuming that distance from shore is a proxy for nutrient availability, these findings suggest that nutrient and sediment input may not be primary contributors to increases in white syndrome (Willis et al. 2004). In fact, several inner shelf reefs relatively close to shore in the Cairns sector had high WSSTA frequencies but very few disease cases in 2002, possibly because host density was also low or because other abiotic or biotic conditions inhibited white syndrome (Willis et al. 2004).

The importance of different abiotic and biotic factors driving white syndrome and other diseases is likely to vary with scale and the host-pathogen system (Bruno et al. 2003). Ocean currents may facilitate spread or isolation of different pathogens (McCallum et al. 2003), but no empirical studies have yet quantified potential dispersal patterns. Biotic factors like host age or size structure are also likely to have significant effects on disease prevalence (Anderson & May 1986; Dube et al. 2002; Lafferty & Gerber 2002). Older or larger hosts may be more vulnerable to disease (Dube et al. 2002; Borger & Steiner 2005), which could be particularly devastating for coral populations where older or larger individuals are likely to have higher reproductive output (Hall & Hughes 1996; Sakai 1998; Dube et al. 2002).

Uncertainty about the identity and source of most pathogens represents a major challenge in understanding the factors that determine pathogen survival and development. Of the currently described coral diseases, only 5 of 18 (Sutherland et al. 2004) have been identified through fulfillment of Koch’s postulates, which require a putative pathogen to be
1) isolated from a diseased individual, 2) grown in pure culture, and 3) transferred to a healthy organism where it induces the disease state (Koch 1882). An additional postulate, that the pathogen be reisolated from the infected organism, was not formulated by Koch, but is also typically recommended (Fredricks & Relman 1996; Richardson 1998; Sutherland et al. 2004). Fulfilling Koch’s postulates for coral pathogens has been challenging, in part due to the complex nature of the host-pathogen relationship, the possibility of multiple disease agents, and the difficulty of natural inoculation (Richardson 1998; Sutherland et al. 2004).

Identifying pathogens through Koch’s postulates is not essential for epidemiological study (Fredricks & Relman 1996), but without isolating pathogens, it has been difficult to determine the mechanisms behind disease dynamics. For example, with a known, cultured pathogen, manipulative experiments on both the isolated pathogen and the host-pathogen system could yield insights into whether temperature is affecting disease by increasing expression of pathogen virulence factors, increasing pathogen growth or reproductive rates, or increasing host susceptibility (Harvell et al. 1999; Harvell et al. 2002).

Although the mechanisms are not known, this study found a strong correlative relationship between white syndrome and warm temperature anomalies. This relationship could have several implications for coral communities on the GBR. White syndrome affects key reef-building species on the GBR including the competitively dominant tabular acroporid corals that constitute a substantial percentage of total coral cover (Baird & Hughes 2000; Connell et al. 2004). Reductions in the abundance of these corals could cause shifts in species assemblages or abundances (Baird & Hughes 2000). In the Caribbean, loss of acroporid corals due to white band disease has led to a shift in dominance to *Agaricia* sp. on some reefs (Aronson et al. 2002) and precipitated a shift to macroalgal dominance on others.
Predicted increases in the frequency and severity of thermal stress anomalies with global climate change (Hoegh-Guldberg 1999) could exacerbate these kinds of disease effects. Our results and the balance of the published evidence from field studies comparing coral disease prevalence among seasons (Edmunds 1991), years (Willis et al. 2004) and sites (Kuta & Richardson 2002) strongly suggest that water temperature plays a substantial role in coral disease dynamics. Because reef building corals are irreplaceable as marine foundation species (Bruno & Bertness 2001), the synergism between temperature and disease could have cascading effects throughout reef ecosystems (Bruno et al. 2003).

**Future research directions**

The development of 21 years of consistently processed satellite sea surface temperature and anomaly data for the GBR region represents a meaningful advancement in understanding the effects of temperature on several parameters of coral health including disease. Further validation of the satellite estimates will provide a better understanding of its limitations and enable more productive and effective use of the dataset. For example, in areas with persistent cloud cover, low data availability may decrease accuracy (Kilpatrick et al. 2001). The relationship of the satellite-measured surface temperatures to temperatures at different depths will depend on bottom topography and the presence of oceanographic features like internal tidal bores (Leichter & Miller 1999), which can alter the temperature regime experienced by corals. Assessing patterns of frequency, extent, and intensity of anomalies over the full time period of the dataset could also identify areas that are more or less vulnerable to thermal stress. The presence or absence of these correlations could help
determine whether marine protected areas can be used to protect areas of greater resilience or resistance to thermal stress (West & Salm 2003; Obura 2005; Wooldridge et al. 2005).

To facilitate regional scale investigations of coral disease risk factors and dynamics, refinement of remote sensing tools must be complemented with rigorous disease monitoring protocols. Much of the current monitoring is idiosyncratic, often in response to a disease outbreak with little baseline or long-term monitoring data (but see Kim & Harvell 2004; Willis et al. 2004; Santavy et al. 2005). Long-term longitudinal and cross-sectional epidemiological studies are an essential component of elucidating density-dependence in disease dynamics, susceptible age classes, possible pathogens or modes of transmission, and potential effects on reproductive output and population dynamics. Monitoring programs intended for use in conjunction with satellite temperature data should sample from different 4 km grid cells as defined by the Pathfinder dataset so that there is adequate replication for analysis. In addition, surveys should be conducted within a relatively close time frame so that the data do not covary with other temporal patterns. Finally, manipulative laboratory experiments are also an essential complement to these correlative studies to identify mechanisms driving correlations between temperature and rates of infection and spread.

Conclusions

Until very recently it was impossible to correlate satellite-derived temperature anomalies with in situ disease surveys. Temporally-consistent satellite temperature data at 4 km resolution enabled us to observe a positive relationship between temperature anomalies and outbreaks of white syndrome at broad spatial scales. A continuing challenge in assessing
the importance of temperature anomalies as factors in disease dynamics will be to measure the role of other variables such as proximity to pathogen sources, local water quality, and physical oceanographic patterns. In some cases, these variables could be more important risk factors than temperature. A priority for coral reef scientists is the implementation of disease surveys on a global scale to adequately test the hypotheses that temperature anomalies and other factors drive coral disease. It is likely that there will be different thermal stress thresholds in different biogeographic regions for each disease. Work is underway to describe disease syndromes worldwide and develop a repeatable method for surveying coral disease (Willis et al. 2004) that can be implemented globally. In combination with satellite temperature data and other data sources, we can then begin to understand disease dynamics at regional scales.
Figure 2.1 Developing the 4 km temperature dataset. An example of the benefits of increasing resolution on the Yucatan peninsula and Caribbean Sea from; (A) 50 km HotSpot data to (B) 9 km Pathfinder data to (C) 4 km Pathfinder data. In the 4 km data, there is less missing data, allowing for greater coverage of coastal areas where many reefs occur. In addition, the 4 km data displays more spatial structure and precision in the temperature values. Data are from January climatological averages, monthly for the 50 km data and from the first week of January for the 9 km and 4 km data.
Figure 2.2 Mean sea surface temperature (°C) from 1985-2003. Averages from this time period were used to create weekly climatologies for each surveyed reef.
**Figure 2.3 Number of white syndrome cases in 2002-2003.** These data were collected by the Australian Institute of Marine Science’s Long-term Monitoring Program. Each of the six latitudinal areas or sectors are labeled with their names and abbreviations. Cooktown / Lizard Island (CL) has nine surveyed reefs, Cairns (CA) has ten, Townsville (TO) has eight, Whitsundays (WH) has nine reefs, Swains (SW) has seven, and Capricorn Bunkers (CB) has four. For each reef, three different sites were surveyed. Disease cases were highest in the Cooktown/Lizard Island and Capricorn Bunkers sectors.
Figure 2.4 Example of white syndrome spreading across *Acropora cytherea*. White areas are coral skeleton that have been recently exposed following die-off behind the disease front.
Figure 2.5 Relationships between the number of white syndrome cases and (A) total percent coral cover (B) and the number of WSSTAs. Solid points in B represent reefs with > 50% coral cover. Each point represents the values from a single reef (n=47).
Figure 2.6 The effect of total coral cover and the number of WSSTAs on the number of white syndrome cases. Values are mean ±1 SE. Values above error bars are the number of surveyed reefs in each of the nine categories.
Figure 2.7  Relationship between mean thermal stress (WSSTAs) and the mean number of white syndrome cases at the sector scale. See Figure 2.3 for sector delineations and abbreviations. Values are mean ±1 SE.
Table 2.1  Relationship between weekly averaged satellite and *in situ* temperatures at nine reefs on the GBR reefs at 5-9 m depth. Field data were collected by the Australian Institute of Marine Science in cooperation with CRC Reef Research Centre and the Great Barrier Reef Marine Park Authority.

<table>
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<tr>
<th>Reef</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Period</th>
<th>n</th>
<th>P</th>
<th>R²</th>
</tr>
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<tr>
<td>Agincourt</td>
<td>-16.0384</td>
<td>145.8688</td>
<td>1996-2004</td>
<td>173</td>
<td>p&lt;.0001</td>
<td>0.91</td>
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<tr>
<td>Chicken</td>
<td>-18.6521</td>
<td>147.7217</td>
<td>1996-2004</td>
<td>244</td>
<td>p&lt;.0001</td>
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<tr>
<td>Davies</td>
<td>-18.8060</td>
<td>147.6686</td>
<td>1996-2004</td>
<td>200</td>
<td>p&lt;.0001</td>
<td>0.96</td>
</tr>
<tr>
<td>Dip</td>
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<td>147.4519</td>
<td>1997-2004</td>
<td>197</td>
<td>p&lt;.0001</td>
<td>0.92</td>
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<tr>
<td>East Cay</td>
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<td>1995-2004</td>
<td>248</td>
<td>p&lt;.0001</td>
<td>0.96</td>
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<tr>
<td>John Brewer</td>
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<td>239</td>
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<td>1996-2004</td>
<td>134</td>
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<td>0.90</td>
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<tr>
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<td>147.3813</td>
<td>1995-2004</td>
<td>205</td>
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<tr>
<td>Turner Cay</td>
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<td>152.5601</td>
<td>1997-2004</td>
<td>204</td>
<td>p&lt;.0001</td>
<td>0.96</td>
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</table>
Table 2.2. Akaike Information Criterion for thermal stress metrics. For each thermal metric we calculated: the AIC, a measure of expected relative Kullback Leibler information; the $\text{AIC}_C$, AIC corrected for small sample size; the difference, $\Delta_i$, between each model and the best model in the set; and the Akaike weight, $w_i$. The sum of all the Akaike weights is equal to 1.0 and each weight represents the approximate likelihood that a specific model is the best model of those compared, in a Kullback-Leibler information sense. For the models that involve a transformed response, likelihoods were adjusted with the Jacobian of the transformation to make the $\text{AIC}_C$ values comparable.

<table>
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<tr>
<th>Metric</th>
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<th>$\Delta_i$</th>
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Acknowledgements

We thank A. Alker, A. Barton, K. France, S. Lee, A. Melendy Bruno, S. Neale, M. O’Connor, N. O’Connor, L. Stearns, all past and present members of the Australian Institute of Marine Science’s Long-term Monitoring Program involved in collecting the disease data, and two anonymous reviewers for their comments. This research was funded in part by the National Science Foundation (OCE-0326705 to J.F.B), an EPA STAR Fellowship to E.R.S, the NOAA Coral Reef Conservation Program and its NESDIS Coral Reef Watch project, and the University of North Carolina at Chapel Hill.
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CHAPTER 3

Evidence of increased resilience to corals from marine protected areas

Abstract

Marine protected areas (MPAs) have become a widely used and effective tool for fisheries management. However, their effects on foundation species like corals, which have declined at unprecedented rates, are not well understood. By restoring historic food web structure, MPAs are hypothesized to benefit corals by increasing resilience to disturbances through the control of macroalgal growth. We tested this hypothesis by compiling spatial databases of MPAs and 8540 coral cover surveys from 4456 reefs around the world. Using a multilevel model, we analyzed how MPAs affect the rate of coral cover change and whether this rate was modified by MPA characteristics like the number of years of protection. Protection in MPAs essentially maintained coral cover over time with trends not significantly different from zero while coral cover on unprotected reefs continued to decline. Within MPAs 53% of reefs experienced increases in coral cover, whereas only 33% of unprotected reefs had increases. In addition, we found that the number of years of protection changed the magnitude of the MPA effect on coral cover, with more years of protection generally resulting in more positive rates of coral cover change. Although these results provide evidence for an effect of resilience on corals in MPAs, the weakness of the MPA effect
underscores the need for additional and more direct conservation measures including those aimed at reducing climate change.

**Introduction**

Continued species loss in a variety of ecosystems has heightened the need for tools to mitigate and manage the effects of human exploitation of natural resources (Chapin *et al.* 2000; Brooks *et al.* 2002). Protected areas, which restrict access or prevent extraction, have become one of the primary tools for species conservation. Although they have long been a mainstay of terrestrial conservation efforts, there has been an increased emphasis on expanding the number of protected areas in the ocean in the past few decades (Agardy 1994; Gubbay 1995), largely due to the worldwide decline of fish stocks (Pauly *et al.* 1998; Worm *et al.* 2005). Marine protected areas (MPAs) are broadly defined as places in the ocean where human activities are restricted. Most MPAs specifically restrict commercial or recreational fishing. However, the continued decline of marine ecosystems has generated renewed interest in using MPAs more broadly for protecting species and restoring ecosystem services (Balmford *et al.* 2004).

MPAs have had success as fisheries management tools (McClanahan & Mangi 2000; Murawski *et al.* 2000). Most research on the effects of MPAs has focused on marine reserves, also called no-take reserves, which prohibit all extractive activities. Research in a variety of marine habitats has shown that the biomass, density, and size of organisms, as well as the diversity of several taxa increased inside reserves (Halpern 2003; Williamson *et al.* 2004). Through protection in MPAs, exploited fish species are able to grow older and bigger
Reserves have also been shown to benefit adjacent fisheries through a spillover effect of larvae and adult fish (McClanahan & Mangi 2000; Roberts et al. 2001; Russ et al. 2004; Murawski et al. 2005). Models indicate that this export of adults and larvae may be able to compensate for the loss of available fishing area (Halpern et al. 2004), but this has not always been found in field studies and may be dependent on the age of the protected area (McClanahan & Mangi 2000).

More recently, MPAs have been proposed as a strategy for reducing coral decline. Globally, coral reefs have undergone a period of rapid, extensive change in the last 20-30 years, which may be unprecedented in the Holocene paleontological record (Aronson & Precht 1997; Aronson et al. 2002; Wapnick et al. 2004; but see Hubbard et al. 2005). Much of the optimism surrounding the effects of MPAs on corals has focused on the theory that a restoration to historic trophic structure, or better management of land-based sources of pollution with inclusion of a terrestrial component, will increase the resilience of coral reef ecosystems to disturbance events (Holling 1973; Grimsditch & Salm 2005; Hughes et al. 2005; Wolanski & De'ath 2005). Resilience is defined as the rate of return to a pre-disturbed state, which is a measure of the persistence of relationships within an ecosystem (Holling 1973). Using MPAs to slow coral decline through a resilience effect is intriguing given the limited range of management options, but it is still largely untested.

Evidence that marine protected areas may have positive effects on coral cover through fisheries management is equivocal. Results from several studies have found that protection in reserves increased the abundance and biomass of grazers that consume macroalgae, which compete with corals (Mumby et al. 2006; Newman et al. 2006; Hughes et al. 2007). Increased grazing can subsequently facilitate greater coral recruitment and
survivorship (Mumby et al. 2007). However, restoration of historic structure may not have predictably positive effects on coral cover. Greater predatory fish abundance from protection in marine reserves could actually result in decreased abundance of herbivorous fish (Hixon & Beets 1993; Graham et al. 2003). Certain fish species may also have negative effects on corals. Although parrotfish are key grazers on macroalgae (Carpenter 1986), they are also corallivorous and can impede coral recovery from disturbance events (Rotjan et al. 2006). In addition, the reduction in algal cover from greater herbivore abundance does not always translate to an increase in coral cover (Jones et al. 2004; Graham et al. 2006; Newman et al. 2006; Ledlie et al. 2007). The effects of reserves on both fish and coral are further complicated by studies that have found that reductions in live coral appear to have led to subsequent reductions in fish abundance and diversity even within MPAs because many fish and invertebrates are obligate or facultative dependents on live coral (Jones et al. 2004).

In spite of these potential benefits, no research has examined whether protection in MPAs can mitigate coral decline through increased ecosystem resilience. Here we use spatial databases of live coral cover surveys and MPA locations to examine whether trends in live coral cover differ systematically inside and outside of MPAs in the Caribbean Sea and Indian and Pacific Oceans. We then determine if attributes of MPAs – size, year of establishment, and World Conservation Union (IUCN) category – affect within-MPA trends. The results of these analyses will help determine if there is evidence of MPAs conferring resilience on coral ecosystems and which characteristics of MPAs may increase a potential positive effect.
Methods

Coral cover surveys

We developed a global database of 8540 surveys, which quantified the percentage of the shallow water hard substratum covered by living hard (scleractinian) coral tissue on 4456 reefs (Fig. 3.1A) from 1969 to 2006. Surveys on 933 of 4456 reefs or 22% of the data were repeated over time. Of the repeatedly monitored reefs, 385 had five or more observations. Data were collected from a variety of sources including peer-reviewed literature, published government and non-governmental organization reports, and existing databases (i.e., Reef Check, Reefs at Risk in Southeast Asia, ReefBase). We used the ISI Web of Science and Google Scholar to find appropriate peer-reviewed and grey literature from management agencies and environmental organizations, targeting our search with the terms "coral" and "cover" and "reef" and "health". We also examined all available issues of journals that were likely to contain coral reef studies including Atoll Research Bulletin, Coral Reefs, Marine Pollution Bulletin, and the Proceedings of the International Coral Reef Symposium. Only surveys above 15 m depth were included to avoid depth biases (for more detail on surveys in the Indo-Pacific regions, see Bruno & Selig 2007).

Marine protected area database

The World Database on Protected Areas (WDPA) maintains a freely available spatial dataset on protected areas worldwide including MPAs (http://sea.unep-wcmc.org/wdbpa). For the Caribbean, some protected areas were updated with data from The Nature Conservancy. In addition, boundaries for the United States' national marine sanctuaries, monuments, and parks were obtained from the National Oceanographic and Atmospheric
Administration, the US Department of the Interior, or the United States Geological Survey where available. We also obtained exact boundaries from the Great Barrier Reef Marine Park Authority for the Great Barrier Reef Marine Park for the pre-2005 zoning, which was the management plan under which all of our data was collected except for one year. Even MPAs which did not have polygon boundaries had data about their area. For the final analysis, 27 of the 311 total MPAs (Fig. 3.1B) analyzed lacked exact boundary information. In these cases, we followed the protocol of similar work (Mora et al. 2006) and delineated a circular buffer around the point to create a boundary of the stated area of the MPA.

Many MPAs (e.g. the Florida Keys National Marine Sanctuary and the Great Barrier Reef Marine Park) contain areas with different IUCN categories or have areas that are spatially disjunct from one another. Therefore, we analyzed the data based on the individual polygons and their associated zoning rather than the name of the larger MPA. The MPA database also contained additional information about the MPAs themselves including their size, IUCN protection category (see Appendix 2.1, Table S2.1), and the year that the MPA was established. Many countries including Australia and the United States have not formally assigned IUCN categories to their MPAs. In these cases, IUCN categories were assigned based on the goals in the management plans and their corresponding level of protection on the IUCN scale. Although the WDPA database had information on the year of establishment for many of these categories, additional data was found by researching government and non-governmental websites.
**Statistical analyses**

We used a multilevel model to examine the relationship between live coral cover and protection over time. Because some surveys were repeated over time, the data could not be considered independent. In addition, reefs were spatially clustered and this autocorrelation had to be accounted for in the statistical model. By using a multilevel model, we were able to include such spatial and temporal structure explicitly (McMahon & Diez 2007). This approach focused on patterns at the scale of individual reefs while still providing population averages for reefs at regional scales (McMahon & Diez 2007). We used the nlme library (Pinheiro et al. 2007) in R 2.5.1 (R Development Core Team 2007) and WinBUGS 1.4.3 (Lunn et al. 2000) to analyze our models.

Percent coral cover is bounded data, which could be described by various probability models including the beta, logistic-normal, and arcsine-normal distributions. We applied a logit transformation to percent coral cover to obtain a logistic-normal distribution, which we then treated as normally distributed (Lesaffre et al. 2007, see Appendix 2.2). We also centered our time regressor in the models we examined. Centering not only reduced correlation between the random effects and facilitated model convergence, but also made the intercept interpretable as the coral cover in the year selected. We found that centering the models on the year 1996 yielded the least degree of correlation between the random effects (Singer & Willet 2003).

**Model development**

We began model development by constructing a generic multilevel model to deal with the spatial and temporal correlation inherent in our data. The assignment of random
effects in a multilevel model accounts for unexplained spatial and temporal heterogeneity. In our model, there were three possible levels, each of which separate observation errors from temporal and spatial effects. At level 1, individual observations on a reef were assigned a unique random effect. Surveys on the same reef over time were assigned a unique random effect at level 2, accounting for temporal correlation. Level 3 contained the spatial unit where protected and unprotected reefs were paired, accounting for spatial correlation.

The spatial units for level 3 were constructed based on MPA boundaries. All reefs within an MPA with the same management criteria were grouped together. Then we paired unprotected reefs with protected reefs based on their distance to the nearest MPA boundary to create reasonably homogenous spatial grouping units. These spatial groupings were used to assign random effects in level 3. We selected the optimal distance using maximum likelihood estimation to compare how a range of distances between 0 and 4000 km influenced the MPA effect on slope (coral cover change). The loglikelihood was maximized at a pairing distance of 200 km (Fig. S2.1). Reefs within 200 km of an MPA were paired with the nearest MPA that contained a coral cover survey; approximately 60% of reefs were paired (see Appendix 2.3 for more details). Any remaining unprotected or protected reefs were left unpaired but grouped into spatial units. For the MPA-only analyses, the spatial groupings were the MPAs.

We began with an ordinary regression model with logit-transformed coral cover (hereafter, logit coral cover) as the response and centered year as the only predictor. We then added temporal structure and spatial structure and used information-theoretic measures (AIC) to conclude that we needed to account for both (Akaike 1973; Burnham & Anderson 2002). The basic trend model fit to each reef is shown in Eqn. (1). In this model, $Y$ is logit coral
cover, $T$ is year, $T_c$ is the centering constant, and $\varepsilon$ is the random error. The subscript $i$
denotes the spatial grouping unit, $j$ denotes the reef within that spatial unit, and $k$ denotes the individual survey measurement for that reef.

Level 1:

$$Y_{ijk} = \beta_{0ij} + \beta_{1ij}(T_{ijk} - T_c) + \varepsilon_{ijk}, \quad \varepsilon_{ijk} \sim N(0, \sigma^2)$$  \hspace{1cm} (1)

The presence of the subscript $j$ in the parameters $\beta_{0ij}$ (intercept) and $\beta_{1ij}$ (slope) indicates that these parameters were allowed to vary from reef to reef. The manner in which they vary is described by the level 2 equation, Eqn. (2).

Level 2:

$$\beta_{0ij} = \beta_{0i} + \beta_{2i}X_{ij} + u_{0ij}, \quad \left[\begin{array}{c}
u_{0ij} \\ u_{1ij}\end{array}\right] \sim N\left(\begin{bmatrix}0 \\ 0\end{bmatrix}, \begin{bmatrix}\tau_0^2 & \tau_{01} \\ \tau_{01} & \tau_1^2\end{bmatrix}\right)$$  \hspace{1cm} (2)

Here, $X$ is a reef-level predictor that varies among reefs but is constant for observations taken on the same reef; $u_{0ij}$ and $u_{1ij}$ are the random effects for reef $j$ in spatial grouping unit $i$ and are assumed to have a joint normal distribution as shown. Protection status (protected versus unprotected) is an example of variable $X$. Random effects from different reefs were assumed to be independent and also independent of the level 1 error terms. The subscript $i$ on the slope and intercept terms in Eqn. (2) indicates that reefs coming from the same spatial grouping unit may also have characteristics in common.

Level 3:

$$\beta_{0i} = \beta_0 + \beta_4Z_i + v_{0i}, \quad \left[\begin{array}{c}v_{0i} \\ v_{1i}\end{array}\right] \sim N\left(\begin{bmatrix}0 \\ 0\end{bmatrix}, \begin{bmatrix}\omega_0^2 & \omega_{01} \\ \omega_{01} & \omega_1^2\end{bmatrix}\right)$$  \hspace{1cm} (3)
In Eqn. (3), Z is a level 3 predictor and the terms $v_{iw}$ and $v_{ij}$ are the error terms. Examples of the variable Z include MPA area, IUCN category or ocean basin. For all models, we included random intercepts and random slopes at levels 2 and 3 (Table S2.2), which allowed trend and coral cover to vary among spatial grouping units as well as among reefs within those units.

**MPA versus non-MPA model**

We began with the basic form of the multilevel model described in Eqns. (1), (2), and (3) and added necessary predictors and spatial structure. As a result of the pairing, the original status of the reef, protected or not, varied with the spatial grouping unit. We treated protection status as a level 2 variable, which could be used to model the level 1 intercept, slope, or both, playing the role of variable $X_{ij}$ in Eqn. (2). Then we fit all possible models that included MPA as a level 2 predictor. Once we selected the appropriate MPA versus non-MPA model using AIC, we explored whether adding a variable that distinguished between ocean basins was needed as a level 3 predictor (Fig. S2.2 compares all the models using AIC). With a model that incorporated protection status as a level 2 predictor, we could determine whether the trend in coral cover varied between protected and unprotected reefs over time.

**MPA-only model**

The MPA-only model used reefs inside MPAs to explore how MPA characteristics—size, IUCN status, or number of years in protection—affect coral cover and its trend over time. For the MPA-only model, we analyzed data from within MPAs to determine which of
the three characteristic variables explained the trend and overall coral cover within MPAs. The number of years of protection was a dynamic variable defined as the number of years the reef was protected at the time of the coral cover survey.

As with the MPA versus non-MPA model, we began with the basic model described by Eqns. (1), (2), and (3) that included random intercepts and random slopes at levels 2 and 3. We then used AIC to compare whether the addition of any of the three variables improved the model (Akaike 1973) either by modifying the slope or intercept. Area and IUCN status varied by the spatial grouping unit (MPA) and were therefore modeled as level 3 variables. Because the number of years of protection at the time of the coral cover survey varied by the individual measurement on a reef, it was modeled as a level 1 variable. We then determined whether adding an additional variable for ocean basin was appropriate.

**Model evaluation**

In order to obtain more realistic estimates of parameter precision, the final AIC best models were refit as Bayesian models in which uninformative priors were used for all parameters. Samples from the parameter posterior distributions were obtained using Markov chain Monte Carlo (MCMC) as implemented in WinBUGS 1.4.3 (for more details see Appendix 2.4). We also summarized the fit of our final model using a modification of $R^2$, the coefficient of determination, generalized to multilevel models (Gelman & Pardoe 2006). In a multilevel model, there are multiple sources of variation to be explained. At each level, we can write $\theta = \mu + \varepsilon$ where $\mu$ is the linear predictor, $\varepsilon$ is the random variation at that level, and $\theta$ corresponds to the individual data points (level 1) or a regression parameter
Eqn. (4) is a generalized version of the equation above for multilevel models:

$$R^2 = 1 - \frac{E(\text{Var}(\varepsilon_{ij}))}{E(\text{Var}(\theta_{ij}))}$$ (4)

In this notation, E is the expectation operator. The expectations in the ratio are calculated by taking the means of the posterior distributions of the variance obtained from a Bayesian fit of the model.

**Results**

*MPA versus non-MPA model*

The best model for analyzing the differences in coral cover trends over time between protected and unprotected reefs included random effects for both the change in coral cover (slope) and intercept at levels 2 and 3. *Protection status* was a significant predictor of both the slope and intercept ($P < .001$). We also found that we needed an additional variable (level 3 predictor), which accounted for the ocean basin of the survey—Pacific Ocean, Caribbean Sea or Indian Ocean. The ocean variable was only needed to modify the intercept (Fig. S2.2 lists the models we fit and compares them using AIC). The AIC best model is shown in Eqn. (5):

$$\logit(p_{ijk}) = \beta_0 + \nu_{hi} + \beta_2 \text{Protection Status}_{ij} + \beta_4 \text{Indian}_i + \beta_5 \text{Pacific}_i + u_{ij}$$

$$+ \left( \beta_1 + \nu_{lj} + \beta_3 \text{Protection Status}_{ij} + u_{lj} \left( T_{ijk} - T_c \right) \right) + \varepsilon_{ijk}$$ (5)
Protection in MPAs resulted in a positive effect on the population-average trend (Fig. 3.2). Change in coral cover was slightly positive but not significantly different from zero in MPAs and negative outside of MPAs (Figs. 3.3, S2.3). We assessed how well individual reef behavior compared to the overall population average using caterpillar plots and found that the slopes generally conform to the model estimates, but the intercepts had more variability (Fig. S2.4). The model explained 46% and 45% of the variation in intercept and slope, respectively, at level 2 and 39% of the variation in intercept at level 3 (Table 3.1).

**MPA-only model**

To determine which characteristics of MPA affected coral cover within MPAs, we examined three variables: year of protection, MPA size, and IUCN category. Based on AIC, MPA size did not improve the model and thus was not included as a predictor. The inclusion of IUCN category as a predictor marginally improved the model, but it had radically different distributions in the three oceans (Tables S2.3-4) and its interpretation in the model was problematic. For example, IUCN models fit separately by ocean did not have an effect, but when the data were pooled across oceans the stricter IUCN categories had a weak positive effect on coral cover. Pooling across oceans yielded a more balanced distribution of data across the IUCN categories. Because the lack of sufficient data in some categories made the model unreliable, we discarded IUCN as a predictor.

The number of years of protection variable significantly improved the model when added as a level 1 predictor. The years of protection variable also had different distributional patterns by year of MPA establishment (Fig. S2.5-6) and by ocean (Fig. S2.7). Unlike the IUCN predictor, though, the effect of years of protection was consistent when all data were
included or if they were separated by ocean. To better capture any ocean differences, we developed two models: one for the Caribbean and one for the Indian and Pacific Oceans (hereafter Indo-Pacific). When we explored different model forms using generalized additive mixed models, we found that a changepoint or breakpoint model (Toms & Lesperance 2003) was needed for the Indo-Pacific (Fig. S2.8A), but the evidence for such a model in the Caribbean was weak (Fig. S2.8B). For the Caribbean, we fit the following linear model (Eqn. 6):

\[
\logit(p_{ijk}) = \beta_0 + \beta_2 Y_{ijk} + v_{oi} + u_{oij} + \left(\beta_1 + \beta_3 Y_{ijk} + v_{li} + u_{lij}\right)\left(T_{ijk} - T_C\right) + \varepsilon_{ijk}
\]  

(6)

In the Indo-Pacific changepoint model, the years of protection effect on trend was different for early and late years. Our final model for the Indo-Pacific (Eqn. 7) described years of protection having a different effect on trend depending on whether the number of years of protection occurs before or after the changepoint:

\[
\logit(p_{ijk}) = \beta_0 + \beta_2 Y_{ijk} + v_{oi} + u_{oij} + \left(\beta_1 + \beta_3 Y_{ijk} + \beta_4 (Y_{ijk} - Y_{CP})^+ + v_{li} + u_{lij}\right)\left(T_{ijk} - T_C\right) + \varepsilon_{ijk}
\]  

(7)

Here \(T\) is the year, \(Y\) is the number of years the reef had been protected at the time of the coral cover survey, \(T_C\) is the centering constant for years, \(Y_{CP}\) is the breakpoint for years protected, and \((Y - Y_{CP})^+\) is the indicator function defined as follows.
We found that the Caribbean and Indo-Pacific models explained 91% and 81% of the variation at level 1, respectively (Table 3.2, Figs. 3.5B-C). To obtain parameter estimates and credibility intervals (hereafter CI), we fit both models in WinBUGS using equivalent parameterizations of Eqns. (6) and (7). The number of years of protection affected the rate of change in coral cover. In the Caribbean, the rate of change in coral cover shifted from negative to positive at 15 years and then began to level off after 30 years (Fig. 3.4A). For the Indo-Pacific, we determined that there were two distinct rates of coral cover change. Using the median of the posterior distribution of the changepoint model, we determined that the switch in the two rates occurred at 21.7 years (20.0-24.9 95% credibility interval). The location of the changepoint was likely the result of a major cohort of reefs, which had been protected for roughly 20 years, experiencing declines due to the 1998 El Niño event. Before the changepoint, the rate of change in coral cover shifted from negative to positive after 5 years and continued increasing until the changepoint at approximately 21 years (Fig. 3.4B). After the changepoint, the rate of change in coral cover became negative again, although not significantly different from zero (Fig. 3.4B).

**Discussion**

Protection in MPAs is widely viewed as a potential way to mitigate the decline of coral reefs (Grimsditch & Salm 2005; Hughes et al. 2005; Sandin et al. 2008). We analyzed
how protection in MPAs affected coral cover on coral reefs globally. MPAs had a weakly positive effect on coral cover rate of change, but coral cover trend was not significantly different from zero. In comparison, unprotected reefs continued to decline (Fig. 3.3).

Annual rates of change depended on the existing coral cover. In 2005, protected reefs in the Pacific and Indian Oceans averaged increases of 0.08% in coral cover. Average coral cover increases were 0.05% in the Caribbean (Fig. 3.3). By contrast, unprotected reefs averaged declines ranging from -0.27% in the Caribbean to -0.43% and -0.41% in the Pacific and Indian Oceans, respectively (Fig. 3.3). In total, 53% of protected reefs had increases in coral cover whereas only 33% of unprotected reefs had increases. Our results suggest that MPAs conferred a weak resilience on corals and that their overall effect was to maintain coral cover, preventing the declines occurring outside of MPAs.

The effect of MPAs on coral cover was dependent on reef location and how long the reef had been protected when it was surveyed. In the Caribbean, coral cover continued to decline for the first 15 years after protection, perhaps due to the time required for fisheries to rebound from exploitation, which has been affecting some areas in the region for several hundred years (Jackson 1997; Wing & Wing 2001). The coral cover trend then became positive and continued to be positive, leveling off at approximately 30 years (Fig. 3.4A). This leveling off pattern is consistent with several studies of protection on reef fish (Maliau et al. 2004; Abesamis & Russ 2005; McClanahan et al. 2007) and at least one field study on coral cover (Halford et al. 2004), which found that populations' recovery reached a saturation point. Because many reef-building corals are slow-growing, recovery rates and leveling off values could vary according to the dominant suite of species on the reef. A rebound in coral cover may also reflect a shift to faster-growing or more stress-tolerant species and a
subsequent change in species composition (Aronson & Precht 1997; Aronson et al. 2004). Shifts in species composition may not only substantially alter the structural complexity of the reef, but also alter the vulnerability of the foundation to disturbances like storms (Madin & Connolly 2006).

In the Indo-Pacific, the effect of the number of years of protection on coral cover displayed two distinct trends. Rates of change in coral cover continued to be negative for the first 5 years, but became positive until approximately 20 years of protection (Fig. 3.4B). At approximately 20 years, coral cover began to decline again and then recovered to a trend that was not significantly different from zero. This reset pattern coincided with a major cohort of reefs that had been protected for 20-25 years when the strong El Niño event occurred in 1998 (Fig. 3.4B). The 1998 El Niño caused high rates of mortality on reefs across the Indo-Pacific region including within MPAs (Arceo et al. 2001; Bruno et al. 2001; Graham et al. 2007). A substantial portion of surveyed reefs in the Indo-Pacific had been protected for 20-25 years in 1998, which was reflected in the transition to a new trend at around 20 years. The Indo-Pacific can experience major mortality events like the 1998 El Niño on a periodic basis (Yu et al. 2006). The recovery and reset in coral cover trend we observed in the 30 years of data we analyzed may be indicative of a cyclical pattern, but establishing a longer-term protection pattern will require more data. For the Caribbean and some years in the Pacific, our MPA-only analyses estimated a more positive effect than seen in the overall MPA versus non-MPA model (Figs. 3.3 and 3.4). Almost 60% of the surveys in our analysis were from MPAs that were less than 15 years old. The young age of many of the studied MPAs means we may be seeing less of a protection effect. Therefore, when the MPA effect was analyzed in aggregate as in the MPA versus non-MPA model, we saw a weaker overall MPA effect.
MPA size can be an important determinant in MPA effectiveness, particularly for mobile species like fish (Claudet et al. in press). We did not find a positive effect of MPA size on coral cover over time. The lack of an effect of MPA size could be due to the relatively short dispersal distances of coral larvae (Ayre & Hughes 2000). Short dispersal distances may mean that even small MPAs may benefit from the larval supply within their boundaries. Synthetic research on MPA effects has also found that even small MPAs can confer positive effects on species biomass and abundance in a variety of marine habitats (Halpern 2003). Although larger MPAs will be able to better protect highly mobile predatory and grazing fish, there is evidence that the benefit increases directly with MPA size. Therefore, protection in small MPAs should still yield a more complete fish assemblage than in unprotected areas (Halpern 2003).

The interpretation of our MPA-specific variables like IUCN category was complicated by the fact that many of the MPAs in our analysis do not have adequate enforcement of their regulations and the categories themselves are self-reported and inconsistent (McClanahan 1999; Burke et al. 2002). We could not exclude poorly managed MPAs from our analysis, because we did not have data on enforcement for most of our MPAs. However, routinely monitored MPAs like the ones that dominate this analysis may be more likely to have had adequate enforcement because they possessed the staff and resources to carry out repeated surveys. Our ability to detect a strong effect of MPAs may also have been compromised by the relatively low percentage of protected coral reefs worldwide. Only 13.4% of reefs are currently protected in non-extractive or multi-use MPAs and only 1.4% are in no-take reserves (Mora et al. 2006). If a greater percentage of reefs
were protected, there could be a positive synergistic effect by having more connected protected populations.

Several additional data issues could have also confounded the results of our analysis. The multilevel modeling approach weights reefs with more time-series data more heavily in the model. Because the Florida Keys National Marine Sanctuary and the Great Barrier Reef Marine Park were the most highly surveyed MPAs in our analysis, our results could have been biased by their overrepresentation in the model. Robustness analyses where we dropped one or both of those subregions indicate that the qualitative outcomes of the model would not change. In addition, the generally less negative trend in coral cover for protected reefs could be due to a more constrained data range within MPAs with cover more likely to increase simply because it was already so low.

Regional and global stressors like increases in ocean temperature and coral diseases are likely to be the greatest counterbalances of positive MPA effects (Berkelmans et al. 2004; Bruno et al. 2007). The weakness of the MPA benefit suggests that in many areas, the effects of these events are overwhelming MPA effects. For example, the GBR experienced major bleaching episodes in 1998 and 2002 with the 2002 episode being the most extensive and severe mass bleaching event on record (Berkelmans et al. 2004). Because these disturbances were relatively recent, it is possible that there was not sufficient time to demonstrate a resilience effect. Yet it seems probable that MPAs subject to broad-scale stressors like increasing ocean temperatures and disease will continue to experience declines in coral cover or fail to attain pre-disturbance coral cover levels.

MPAs can play a critical role in the protection of coral reef ecosystems, particularly fisheries (Russ & Alcala 2003). Contextualizing the success of MPAs will require analyzing
other metrics of resilience including species abundance and richness of other reef taxa
(Bellwood et al. 2006). Changes in coral or fish species assemblages could have far-reaching
effects on the structure and function of coral reef ecosystems (Aronson et al. 2004; Wilson et
al. 2006). Our analysis indicated that MPAs can help to maintain coral populations.
However, the weakness of the effect suggests that it may not be enough to offset coral losses
from major disease outbreaks and bleaching events, which are both predicted to increase in
frequency with climate change (Sheppard 2003; Ward & Lafferty 2004; Sheppard & Rioja-
Nieto 2005). MPAs have long been acknowledged to be an effective yet imperfect response
to anthropogenic threats (Allison et al. 1998; Lubchenco et al. 2003). Reversing coral
decline will require both the local management of stressors through MPAs and international
policies aimed at reducing the human activities causing climate change.
Figure 3.1 Location of unprotected (orange) and protected (green) coral cover surveys in the (A) Caribbean and (B) Indo-Pacific (not pictured: Central Pacific and Eastern Indian Ocean reefs).
Figure 3.2 Coefficient estimates for the MPA versus non-MPA model. The 95% credibility intervals (thin grey line) and the 50% credibility intervals (thick black line) as well as point estimates (median) of the posterior distributions for all parameters in the MPA versus non-MPA model using a Bayesian approach to fit the model in Eqn. (1). There is a 95% probability that the true value lies within the 95% credibility interval. The MPA x 10-Year Trend term should be contrasted with the 10-Year Trend term, which is the trend for non-MPAs. The MPA x 10-Year Trend term is an effect and gets added to the 10-Year Trend term when MPA = 1 to obtain the trend for MPAs.
Figure 3.3 The change in percent coral cover from 2004 to 2005 inside and outside of MPAs. The 95% credibility intervals (error bars) are also shown. Reefs protected in MPAs had slightly positive changes in coral cover, although not significantly different from zero (dashed line). Percent coral cover was obtained by back-transforming the predicted logit from the model.
Figure 3.4 The effect of the number of years of protection on the 1-year change in coral cover. The 95% credibility intervals (dark grey bands) and the 50% credibility intervals (light grey bands) as well as the median (white line) of the posterior distributions for the year of protection models in the (A) Caribbean and (B) Pacific and Indian Oceans in 1996.
Figure 3.5 Comparisons of the average coral cover per year as predicted by the models, in simulated data sets (light grey lines) with the observed mean coral cover per year (thick black line) for (A) MPA versus control model, (B) MPA-only Caribbean years of protection model, and (C) MPA-only Indo-Pacific years of protection model. The histograms at the bottom of the figures display the relative sample sizes at each year for the actual data. Note that the x-axes differ for the plots due to data availability.
Table 3.1 \( R^2 \) for MPA versus non-MPA model. NA denotes the lack of predictor for calculation \( R^2 \).

<table>
<thead>
<tr>
<th>Model level</th>
<th>( y ) (logit coral cover)</th>
<th>intercept</th>
<th>slope</th>
</tr>
</thead>
<tbody>
<tr>
<td>Level 1</td>
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<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Level 2</td>
<td>—</td>
<td>0.46</td>
<td>0.45</td>
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<tr>
<td>Level 3</td>
<td>—</td>
<td>0.39</td>
<td>NA</td>
</tr>
</tbody>
</table>
Table 3.2  $R^2$ for MPA-only models in (A) Caribbean and (B) Indo-Pacific. $R^2$ can only be calculated at level 1 for these models.

<table>
<thead>
<tr>
<th></th>
<th>$y$ (logit coral cover)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caribbean</td>
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</tr>
<tr>
<td>Indo-Pacific</td>
<td>0.80</td>
</tr>
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</table>
Acknowledgments

T. Jobe, J. Lang, M. O'Connor, J. Weiss, P. White for helpful comments on the manuscript.
References


CHAPTER 4

Temperature-driven coral decline: do marine protected areas have a role?

Abstract

Climate change is predicted to have devastating impacts on coral reef health. One proposed conservation strategy for managing the effects of climate change on coral reef ecosystems is the use of marine protected areas (MPAs). This strategy assumes that MPAs can indirectly protect coral populations from ocean warming through fisheries management and reductions in terrestrial run-off. Using temperature anomaly and coral cover databases, we quantified the effect of temperature anomalies and MPA protection on the trend in coral cover from 1987-2005 globally. Protection did not mitigate the negative effect of warm temperature anomalies on coral cover. In addition, the magnitude of the MPA benefit was generally not enough to compensate for the negative effect of temperature anomalies on coral cover. MPAs also did not capture the natural range of temperature variability on reefs. The current placement of MPAs overprotects areas with very few temperature anomalies and underprotects areas with moderate numbers of anomalies. Field research suggests that locations with moderate anomalies may be more acclimated to thermal stress and better able to withstand bleaching. If MPAs are located more strategically to protect naturally acclimated populations, protection may provide a synergistic benefit. However, the failure of MPAs to lessen the negative effect of thermal stress on coral cover suggests that although
MPAs are important conservation tools, they need to be complemented with additional policies aimed at reducing the activities responsible for climate change.

Introduction

The pervasiveness of climate change presents unique challenges for resource management. Traditional management tools like parks and reserves have the potential to be effective in restoring endangered populations, preventing habitat destruction (Bruner et al. 2001), and preserving ecosystem services (Balmford et al. 2002). However, climate change is expected to alter the physical factors necessary for habitat development, complicating management within static boundaries like parks or protected areas. Within park boundaries, changes in temperature and precipitation may shift species ranges and abundances potentially threatening the persistence of the ecosystem itself (Parmesan & Yohe 2003). Through distribution shifts and fundamental changes in community structure, non-dynamic protected areas could end up failing to even include the species or ecosystems they were designed to conserve.

In spite of these challenges, there is still optimism that protected areas can be useful for conservation in the face of climate change if they can increase ecosystem resilience. Ecosystem resilience (sensu Holling 1973) is broadly defined as the rate of return to a pre-disturbed state, a measure of the persistence of relationships within an ecosystem. Marine protected areas (MPAs) are thought to be able to increase resilience to climate change by directly mitigating other stressors like overfishing (Hughes et al. 2003; Grimsditch & Salm 2005). In addition, it is theorized that conservation benefits can be maximized by protecting
naturally resilient areas, which have higher diversity or connectivity (Gunderson 2000; Bengtsson et al. 2003; Hughes et al. 2003; West & Salm 2003; Bellwood et al. 2004; Adger et al. 2005). If protected areas can enhance ecosystem resilience, they may be able to moderate climate change effects by creating the conditions necessary for recovery from disturbances.

To date, much of the speculation about the use of protected areas to increase resilience to climate change effects has focused on coral reef ecosystems (Hughes et al. 2003; West & Salm 2003; Bellwood et al. 2004; Obura 2005; Wooldridge et al. 2005). Climate change could threaten coral reef ecosystems through rising sea levels (Blanchon & Shaw 1995) and ocean acidification (Hoegh-Guldberg et al. 2007). In the short-term, though, corals are particularly vulnerable to climate change because reef-building corals already live near their upper thermal limits (Jokiel & Coles 1990). When corals experience temperatures more than 1°C beyond typical maximum summertime averages, they can lose their symbiotic algae or zooxanthellae in a process known as coral bleaching (Glynn 1993). Although corals can recover from bleaching in response to relatively short and weak temperature anomalies, prolonged high temperatures like those associated with the 1998 El Niño can cause extensive bleaching and mortality on individual reefs (Arceo et al. 2001; Bruno et al. 2001; Graham et al. 2007). Warm temperature anomalies also triggered subsequent mass bleaching events in 2002 on the Great Barrier Reef and 2005 in the eastern Caribbean (Berkelmans et al. 2004; Whelan et al. 2007). Most climate change scenarios predict an increase in the frequency and severity of these thermal stress events (Hoegh-Guldberg 1999; Sheppard 2003; Sheppard & Rioja-Nieto 2005).
Marine protected areas (MPAs) have been proposed as tools for mitigating the effects of warm temperature anomalies by reducing or eliminating fishing. Prohibiting fisheries exploitation in temperate and coral reef MPAs has been shown to restore natural trophic structure (Shears & Babcock 2003; Guidetti 2006; Mumby et al. 2007a). Recent work has found that individual MPAs can have a positive effect on coral cover through trophic cascades, which limit algal growth and facilitate coral recruitment (Mumby et al. 2006; Mumby et al. 2007b). Large scale analyses have also found that protection in MPAs maintained coral cover levels over time, while unprotected reefs continued to decline (Selig & Bruno in prep).

However, studies supporting the hypothesis that MPAs could be useful in conservation efforts to protect corals from thermal stress are equivocal and generally restricted to single reserves. A more complete suite of herbivorous fish could theoretically suppress macroalgal growth following bleaching events. After bleaching events, algae can colonize dead coral skeleton (Diaz-Pulido & McCook 2002), potentially reducing coral settlement (Birrell et al. 2005) and suppressing coral growth (River & Edmunds 2001). Nonetheless, the effects of a restoration to historic trophic structure are not well understood and may not necessarily facilitate coral recovery after thermal events. An analysis of Cousin Island Marine Reserve in the Seychelles found little recovery from major coral mortality following the 1998 El Niño event in spite of unchanging high herbivore abundance over the study period (Ledlie et al. 2007). In addition, Jones et al. (2004) found that protection did not mitigate a decline in coral cover or a subsequent decline in coral-dependent fish. From these studies, it remains unclear whether the reduction in fishing in MPAs can increase recovery from thermal stress at regional scales.
Globally, the oceans have warmed $0.52^\circ C \pm 0.19^\circ C$ between 1850 and 2004 with some regional variability (Casey & Cornillon 2001; Rayner et al. 2006). If warming continues at a similar rate, current thermal limits for most corals will be exceeded in the next 100 years without rapid acclimation or adaptation (Donner et al. 2005; Hoegh-Guldberg et al. 2007). Even rises of $0.1^\circ C$ could increase the geographic extent of bleaching in the Caribbean by 42% (McWilliams et al. 2005). Therefore, testing whether MPAs can be useful in mitigating temperature-associated coral loss is critical so that we can determine what management interventions are needed before there is further loss. At least one strategy suggests that placing MPAs in locations with specific temperature profiles may increase overall coral reef ecosystem resilience (West & Salm 2003; Grimsditch & Salm 2005). Data are needed for assessing whether these strategies could work and for guiding management decisions about designing MPAs with the goal of reducing the effects of thermal stress.

We used spatial databases on temperature anomalies (Selig et al. in prep), MPAs, and live coral cover to test whether locations with similar numbers of temperature anomalies experienced fewer declines in coral cover inside MPAs than in unprotected areas. Failure to mitigate the effect of temperature anomalies could be explained by at least two factors. If MPAs are too small, they may be susceptible to widespread mortality from a single anomaly event and not have enough healthy populations to restore degraded areas. Therefore, we analyzed patterns in temperature anomaly areas to compare them with MPA areas. In addition, if MPAs are not protecting natural temperature variability on reefs, they may have populations that are less thermally tolerant to stress. We assessed whether temperature anomaly patterns of reefs within MPAs were similar to those of all reefs. With this analysis, we were able to determine if MPAs were disproportionately protecting reefs with low,
Methods

Temperature anomaly database

We created a 21-year dataset of temperature anomalies covering the entire range of tropical reef-building corals (37°N to 37°S) using the National Oceanic and Atmospheric Administration’s (NOAA) National Oceanographic Data Center and the University of Miami’s Rosenstiel School of Marine and Atmospheric Science Pathfinder Version 5.0 temperature data (http://pathfinder.nodc.noaa.gov). These data have the highest spatial resolution for the longest time period of any publicly available satellite temperature data. To avoid diurnal biases (Casey 2002) and reduce the number of missing pixels by 25%, we averaged the day and night measurements. In addition, we used data with a quality flag of 4 or better (Casey & Cornillon 1999; Kilpatrick et al. 2001). We initially filled the remaining data gaps (21.2% of the data) using a 3 x 3 pixel median spatial fill; remaining gaps were filled temporally using the Piecewise Cubic Hermite Interpolating Polynomial (PCHIP) function in Matlab (The Mathworks Inc. 2006). Climatologies were created using a harmonic analysis procedure to fit the annual and semi-annual signals to the time-series at each grid cell location (Selig et al. in prep).

We defined thermal stress anomalies (TSA) as deviations of 1°C or greater from the temperature during the mean maximum climatological week from 1985-2005. The mean...
maximum climatological week is the long-term average warmest week. Although specific temperatures that cause coral bleaching and mortality are highly species-specific (Fisk & Done 1985; Lang et al. 1992; Glynn 1996; Berkelmans & Willis 1999; Marshall & Baird 2000; Loya et al. 2001), this is a generally accepted threshold for conditions that may result in bleaching (Glynn 1996; Liu et al. 2003; Berkelmans et al. 2004).

**Quantifying patterns in anomaly areas by region**

We analyzed patterns in anomaly area throughout the tropics and by region to determine anomaly area statistics for geographic areas with similar diversity or management (Fig. 4.1). These regions roughly correspond to marine ecoregions designated by non-governmental organizations for conservation priority setting (Spalding et al. 2007). Analyses were done by region because different oceanographic patterns may lead to variability in anomaly areas. Knowing how anomaly areas vary by region can give managers and policymakers more precise data for their location. To determine anomaly areas, we first created 1096 spatial grids of anomaly presence and absence for each week of the 21-year temperature anomaly database. Only anomalies which contained at least one pixel that overlapped a known coral reef location were included. We used the Image Processing Toolbox in Matlab 7.3 (bwlabel function) to identify each anomaly and determine whether it was connected to a neighboring thermal event in any of the eight adjacent pixels (The Mathworks Inc. 2006). Each contiguous temperature anomaly group was assigned a unique number from which we calculated the total area of the group and the mean, maximum, and variance in area size for each time step and region.
**Marine protected area and coral reef databases**

We built a spatial database of marine protected areas primarily using data from the publicly available World Database on Protected Areas 2005 (WDPA Consortium 2005). These data were then supplemented and updated with MPA data from The Great Barrier Reef Marine Park Authority, The Nature Conservancy, NOAA, the US Geological Survey and the US Department of Interior. Most of the MPA data had exact boundaries, but some locations had only information about the center latitude and longitude point of the MPA location. Of the 298 MPAs used in this analysis, approximately 25 had information on total area but not actual boundaries. The extent of these areas had to be approximated and area calculations represent estimates based on the best available data. For areas in which we only had point data, we created artificial circular boundaries based on the total known area of the MPA (Mora et al. 2006). Because we were interested only in coral reef MPAs, we selected only parks that fell within 50 km of a known coral reef location. Coral reef location data varies in quality for much of the world, but we compiled known locations from Reefbase (www.reefbase.org), Reefs at Risk (Bryant et al. 1998), Reefs at Risk in Southeast Asia (Burke et al. 2002), and Reefs at Risk in the Caribbean (Burke & Maidens 2004).

**Live coral cover database**

We developed a live coral cover database from several publicly available databases (Reef Check, ReefBase, and Reefs at Risk in Southeast Asia) as well as peer-reviewed and grey literature. To find relevant articles, we searched the ISI Web of Science and Google Scholar with the terms "coral" and "cover" as well as "reef" and "health". We also examined all available issues of journals that were likely to contain coral reef studies including *Atoll*
Research Bulletin, Coral Reefs, Marine Pollution Bulletin, and the Proceedings of the International Coral Reef Symposium. In general, the surveys used some variant of the line transect technique. We only used data from 15 m depth or above to avoid depth biases in coral cover. Our final global database contained 8040 surveys over 4260 reefs from 1987-2005.

Statistical analyses

Multilevel model development

We used a multilevel model to evaluate whether protection in MPAs changed coral cover responses to thermal stress from 1987-2005 compared to unprotected corals. By using a multilevel model, we were able to estimate how protection and thermal stress drove variability in coral cover over time on each reef as well as a population average for all reefs. The multilevel modeling approach also allowed us to account for the temporal and spatial correlation in the data (McMahon & Diez 2007). At each level we assigned different random effects to account for spatial and temporal correlation. For example, at level 1, individual observations on a reef were assigned a unique random effect. At level 2, the random effect accounted for repeated surveys on the same reef over time. Level 3 accounted for spatial correlation within the spatial grouping unit where protected and unprotected reefs were paired. Unprotected reefs were paired with the nearest protected area that contained coral reef surveys up to a distance of 200 km (see Selig & Bruno in prep for full methods). Then we applied a logit transformation to the percent coral cover data and treated the logit as normally distributed (Lesaffre et al. 2007). We also centered our time regressor at 1996 to facilitate model convergence, provide an interpretable intercept, and to minimize correlation
among random effects (Singer & Willet 2003). Centering is the equivalent of examining changes relative to a chosen reference year, in this case, 1996. We used the nlme library (Pinheiro et al. 2007) in R 2.5.1 (R Core Development Team, 2007) and WinBUGS 1.4.3 (Lunn et al. 2000) to analyze our models.

After determining the basic model structure, we explored how to incorporate temperature into the model. Studies suggest that there can be a temporal delay from the beginning of a temperature anomaly to a biological response in coral cover or fisheries (Graham et al. 2007). Therefore, we examined models with no lag and variations of 1, 2, and 3 year lags. Using Akaike Information Criterion (AIC) we found that a variable that contained the number of weekly anomalies in the 2 calendar years preceding the year of each coral cover survey (lag TSA) best explained variation in coral cover (Akaike 1973).

The basic trend model Eqn. (1) we fit to each reef described logit coral cover ($Y$) in terms of year ($T$) and its centering constant ($T_c = 1996$), the number of anomalies in the 2 years preceding the coral cover survey (lag TSA) and the random error ($\varepsilon$). The subscripts $i$, $j$, and $k$ designate the spatial unit for pairing MPA and non-MPA reefs, the reefs within that unit, and the individual survey measurement for that reef, respectively.

$$ Y_{ijk} = \beta_{0ij} + \beta_{1ij}(T_{ijk} - T_c) + \beta_{2ij}\text{lag TSA}_{ijk} + \varepsilon_{ijk}, \; \varepsilon_{ijk} \sim N(0,\sigma^2) $$ (1)

The subscript $j$ appearing in the parameters $\beta_{0ij}$ (intercept), $\beta_{1ij}$ (trend), $\beta_{2ij}$ (lag TSA) signifies that these parameters are allowed to vary from reef to reef. Their variability is described in Eqn. (2):
Here, *Protection status* is a reef-level predictor that varies among reefs (protected versus unprotected) but is constant for observations taken on the same reef. Random effects for reef *j* in spatial unit *i* (*u_{0ij}, u_{1ij},* and *u_{2ij}* ) are assumed to have a joint normal distribution as shown.

*Protection status* is a dummy variable where 1 = protected and 0 = unprotected. Random effects from different reefs are assumed to be independent and also independent of the level 1 error terms. The subscript *i* on the trend, *lag TSA*, and intercept parameters, as well as the coefficients of the level 2 predictor *Protection Status*_{ij} in Eqn. (2) indicates that these parameters can vary across spatial units as described by Eqn. (3):

\[
\begin{align*}
\beta_{0i} &= \beta_0 + \beta_s Indian_i + \beta_P Pacific_i + v_{0i} \\
\beta_{1i} &= \beta_1 + v_{1i} \\
\beta_{2i} &= \beta_2 \\
\beta_{3i} &= \beta_3 \\
\beta_{4i} &= \beta_4
\end{align*}
\]

(3)

In Eqn. (3), we included ocean basin as a level 3 predictor because earlier modeling efforts (Selig & Bruno *in prep*) and different temperature patterns in the different basins indicated that coral cover may be modified by ocean basin. The Caribbean serves as the baseline level
in this model and corresponds to Pacific = Indian = 0. Random effects for level 3 are designated by $v_{o_i}$ and $v_{i_t}$.

To develop a final model, we determined the basic level-1 model, added random effects where statistically necessary, and then added additional predictors (Protection status and ocean). We tried several variations on the basic level-1 model shown in Eqn. (1) including the interaction of time (coral cover trend) and lag TSA, but rejected them using AIC. By fitting models to individual reefs, we observed that intercepts (logit coral cover in 1996) varied widely across reefs and spatial grouping units, whereas coral cover trend coefficients were less variable and lag TSA coefficients had almost no variability. Random effects account for unobserved heterogeneity in the model so we included random effects only for the intercept and trend. Then we determined how to add Protection Status and ocean as predictors, using AIC to identify which model was the best fit model (Akaike 1973). To obtain more realistic estimates of parameter precision and credibility intervals, we refit the final model as a Bayesian model with uninformative priors in WinBUGS 1.4.3 (Lunn et al. 2000). Credibility intervals are the range within which there is a defined probability that the true value lies. For example, within a 95% credibility interval, there is a 95% probability that the true value lies within the given calculated range.

**Monte Carlo simulations**

We used Monte Carlo simulations to test whether or not temperature anomaly patterns varied significantly between reefs in MPAs and all reefs. For this analysis, we focused on 7 years of interest: 1985, 1988, 1995, 1998, 2000, 2002, and 2005. The years 1988, 1998, 2002, and 2005 were selected because they were El Nino years (1988, 1995,
1998, and 2002) or years with a documented major thermal event (2005). We included 1985 and 2000 as reference years. To assess whether the temperature anomaly patterns exhibited by reefs in MPAs are typical of all reefs, we first treated all reefs including those within MPAs to be a theoretical population. We then drew 10,000 random samples of size 10,555 (the number of 4 km reef pixels in MPAs that matched the temperature database pixels) from this theoretical population of 55,626 reefs. For each sample, we calculated the variance, interquartile range (IQR), median absolute deviation (mad), mean and median. The frequency distribution of each summary statistic calculated from the random samples was then used to estimate the sampling distribution of that statistic. The observed value of the statistic for MPAs was compared to the theoretical population distribution of that statistic to determine if the MPA value was typical. We then used Pearson's $\chi^2$ Goodness of fit test to get more specific information about how the general reef and MPA distributions varied. Because of our large sample size, formal significance testing would virtually guarantee finding a significant lack of fit. However, we were able to use the Pearson residuals to determine which temperature anomaly categories were driving the lack of fit.

**Results**

**Effect of protection and temperature anomalies on coral cover**

The best model described coral cover as a function of time, thermal stress, protection, and ocean. *Protection status* (a level-2 predictor) modified both the change in coral cover and intercept (coral cover in 1996, the centering year), while ocean basin affected only the intercept (level 3 predictor). Random effects were necessary for both reefs and spatial grouping units. Using an AIC framework, we found the best model to be given by Eqn. (4):
We found that protection in MPAs did not mitigate the effect of temperature anomalies on coral cover (Figs. 4.2-4.3). As with previous work, MPA status had a significant effect on the direction and magnitude of coral cover trend (Selig & Bruno in prep). The trend outside MPAs was negative, indicating a decline in coral cover over time. Within MPAs, though, the coral cover trend was weakly positive, although not significantly different from zero (Fig. 4.2). However, when we fit a model that allowed MPA to modify the effect of temperature anomalies on coral cover, the interaction term was not significant (p>0.1) and the model was not a better fit in an AIC context. Therefore, MPAs did not modify the effect of thermal stress on coral cover (Fig. 4.3). In other words, MPAs may benefit corals through the mitigation of other stressors (i.e., overfishing and terrestrial inputs), but they are not specifically altering the effect of temperature anomalies on coral cover.

Temperature anomalies had a significant negative effect on coral cover (P<.0001), although this finding is consistent with numerous studies relating temperature anomalies to bleaching and coral mortality (Arceo et al. 2001; Bruno et al. 2001; Berkelmans et al. 2004), our model quantified the general rate of coral cover loss as a function of the number of temperature anomalies (Fig. 4.4). For example, across reefs, 8 anomalies of more than 1°C above summertime averages were correlated with a 3.9% loss in coral cover.

\[
\text{logit}(p_{ijk}) = \beta_0 + \nu_{ui} + \nu_{2i} + \beta_{2j}TSA_{ijk} + \beta_{3j}MPA_{ijk} + \beta_{7}Indian_{i} + \beta_{8}Pacific_{i} + \mu_{0ij} + \mu_{2ij} + \left( \beta_1 + \nu_{li} + \beta_{4i}MPA_{ij} + \nu_{1ij} \right)(T_{ijk} - T_c) + \epsilon_{ijk}
\] (4)
Temperature anomaly patterns of MPAs versus all reefs

Protected reefs experienced less thermal stress than the general population of reefs. Weekly temperature anomaly patterns in MPAs did not represent a random sample of those on all reefs. For the years studied, MPAs had more reefs with low numbers of anomalies (0-1) than the general population of reefs. MPAs also included fewer reefs with moderate anomaly frequencies (2-6). This result does vary among years and 1998 and 2002 were exceptions to the overall pattern. During the 1998 El Niño, MPAs underrepresented reefs with low numbers of anomalies, overrepresented reefs with anomaly frequencies 1-5 and underrepresented reefs with moderate numbers of anomalies (6-12). In addition, the 1998 event was the most deviant from a random sample of temperature anomalies with nearly every anomaly category exceeding the Pearson critical value. In contrast, low anomaly numbers (0-2) were underrepresented in MPAs in 2002 and there was an overrepresentation of moderate numbers of anomalies (3-8). For each year, we took the 95% percentile-based confidence intervals from the Monte Carlo simulations and compared them to MPA anomaly patterns. From these analyses, we determined that MPAs generally had lower mean anomaly values (Fig. 4.5A) and lower standard deviations (Fig. 4.5B) than all reefs. Our results suggest that locations protected within MPAs experience different temperature patterns than all reefs and do not contain the natural range of temperature variation.

Patterns in anomaly area

The overall event size anomaly distribution illustrates that 70% of anomalies are less than 75 km², but that a few anomalies are over 1,000,000 km². Anomaly event sizes varied annually and regionally (Figs. 4.1 and 4.6). At a regional scale, variability in the size of
smaller anomalies was generally low (under 100 km²). Most of the variability occurred in
the tail of the distribution where there were few large anomalies (Fig. 4.6). Contrary to
expectations, the size of the region seemingly did not affect the pattern of anomaly sizes.
The smallest region in the analysis, the Florida Keys, also had some of the largest anomaly
sizes. More size variability was present in Pacific regions that are affected by El Niño events
(Fig. 4.6).

Discussion

The success of marine protected areas (MPAs) in restoring fisheries on coral reefs
(Alcala et al. 2005; McClanahan et al. 2007c) has led to increased optimism that they may
also be useful for mitigating temperature stress associated with climate change (Sandin et al.
2008). However, our global analysis found that there is no evidence to suggest that MPAs
are reducing the effects of temperature anomalies on coral cover in general. Although MPAs
helped to reduce coral decline, they did not modify the effect of thermal stress on coral cover
(Fig. 4.3).

The effects of temperature anomalies on bleaching rates and coral cover on individual
reefs have been widely documented (Glynn et al. 1988; Goreau & Hayes 1994; Arceo et al.
2001; Bruno et al. 2001; McClanahan et al. 2007b). However, the general relationship
between the number of temperature anomalies and the percentage loss in coral cover has not
been described. We found a negative relationship between the number of anomalies and
change in coral cover (Fig. 4.4A). The degree of percent coral cover loss depended on the
number of anomalies and the starting coral cover (Fig. 4.4A). For example, at 50% coral
cover, 4 anomalies resulted in coral cover losses of approximately 2% (Fig. 4.4B). Bleaching as a result of temperature anomalies is highly species- and location-specific (Berkelmans & Willis 1999) and mortality on a given reef can approach 90% during episodes of high anomaly frequency or magnitude (Graham et al. 2006). Clearly bleaching rates on individual reefs can be highly idiosyncratic, but our results suggest that there was a general relationship between the number of temperature anomalies, coral cover at that time, and percent coral cover lost during thermal events.

In addition, when the magnitude of coral loss as a result of temperature anomalies was compared to the magnitude of the positive effects of MPAs, our results indicated that MPAs alone may not be sufficient to mitigate coral loss due to temperature anomalies. Under optimal conditions, MPAs generally resulted in increases in coral cover of 1-2% per year (Selig & Bruno in prep). Therefore, the balance between coral loss from temperature anomalies and the benefits from MPAs are unlikely to produce a net gain in coral cover over time on most reefs.

Several factors could explain the failure of MPAs to protect against thermal stress. One possibility is that MPAs are currently not optimally designed because of their placement or their size. One conservation scheme prescribes protecting populations that have had a history of little or no temperature stress and populations that have had only moderate levels of stress (Grimsditch & Salm 2005). When we compared the thermal profiles of the current set of MPAs to the general population of all reefs, we found that MPAs had a significantly different number of anomalies from the distribution of anomalies on all reefs. In fact, MPAs disproportionately protected low anomaly frequency areas. These areas of low thermal stress likely result from local oceanographic conditions like upwelling. However, field research
suggests that populations that have not been subjected to temperature anomalies undergo greater mortality when they do experience thermal stress (McClanahan et al. 2007a).

Including sites with a history of more moderate numbers of temperature anomalies may be necessary for developing a set of MPAs capable of slowing or reversing coral decline because these locations contain more acclimated corals. Coral acclimation and adaptation to thermal stress through exchange of their zooxanthellae is routinely invoked as a possible mechanism for corals to survive increases in ocean temperature (Baker 2001; Coles & Brown 2003; Baker et al. 2004; Fautin & Buddemeier 2004). Successful acclimation or adaptation could occur through the acquisition of thermally-tolerant zooxanthellae, potentially during warm water events that result in non-lethal bleaching (Fautin & Buddemeier 2004). For several years during our study period, MPAs had substantially lower anomaly frequencies and less temperature variability than all reefs (Fig. 4.5B). An analysis of field sites in East Africa found that sites which had more temperature variability experienced less mortality during thermal stress events (McClanahan et al. 2007a). Therefore, the lack of representation of reefs with more temperature variability and moderate numbers of anomalies in MPAs could partially explain why protection does not modify the effect of warm temperature anomalies on coral cover.

In addition, our analysis of anomaly sizes suggests that MPAs may be too small to adequately protect against thermal stress. A key component of protected area design has been to create reserves larger than the typical natural disturbance regime so that enough species and ecosystem function remain to recover from disturbances (Pickett & Thompson 1978). We found that anomalies varied considerably in size based on region and year. Most anomaly events are relatively small, but the overall distribution usually includes a small
number of large area, particularly during major events like the strong El Niño in 1998 when a few weeks had anomaly sizes that exceeded 1 million km$^2$. Because no MPA can encompass such a large contiguous area, managers may need to design MPAs to insure against a reasonable degree of thermal stress rather than a maximum by constructing MPAs to be larger than an acceptable percentage of anomaly events (Fig. 4.6). For example, in the Western Indonesia region, an MPA greater than 50 km$^2$ would be larger than 50% of anomaly events and at 150 km$^2$, it would be larger than 75% of anomaly events. Currently, about 40% of coral MPAs are 1-2 km$^2$ (Mora et al. 2006), considerably smaller than a typical anomaly. Therefore, most MPAs are likely to be wholly affected by a single anomaly event. Larger MPAs could confer greater resilience from thermal anomaly events because they would be more likely to contain unaffected populations within their boundaries. These population might then be able to reseed those that had experienced mortality during the event (Grimsditch & Salm 2005).

Regardless of MPA design, a resilience effect of MPAs on coral cover can only be mediated indirectly through the two stressors that MPAs can directly affect. MPAs have direct effects on coral reef fish populations through the restoration of historic abundance and age structure (McClanahan & Mangi 2000; Roberts et al. 2001; Halpern 2003; Russ et al. 2004; Williamson et al. 2004). They can also have local direct effects on the reduction of nutrients and sediments if they include a terrestrial component (Grigg 1995; Wolanski & De'ath 2005). Through the mitigation of these stressors, MPAs can provide a mechanistic indirect benefit to corals (Mumby et al. 2007a; Selig & Bruno in prep). Coral cover is an important metric of resilience because live coral provides the foundation structure for the entire reef ecosystem and many reef taxa are dependent on its framework (Bruno & Bertness...
However, other metrics of resilience may also be indicative of reef health including coral size, coral and fish diversity, fish abundance, macroalgal cover and connectivity to other reef communities (Bellwood et al. 2003; Birrell et al. 2005; Grimsditch & Salm 2005; Hughes et al. 2007; McClanahan et al. 2008).

Biophysical models and field studies will be needed to determine the mechanisms and role of other potential sources of coral reef resilience.

Researchers predict that the thermal limits of corals will need to increase at rates of 0.2–1.0°C per decade to avoid mass bleaching and mortality (Donner et al. 2005). Whether corals can keep pace with such rates through mechanisms such as adaptive bleaching is unclear (Sheppard 2003; Sheppard & Rioja-Nieto 2005). Our results caution against relying on MPAs to substantially alter the course of climate change-induced coral degradation. The benefits of MPAs to fisheries are clear and the restoration to more intact trophic structure may explain the small benefit MPAs provide to corals. Nevertheless, MPAs do not specifically mitigate the effect of warm temperature anomalies on coral cover. Some of the weakness of the MPA effect could be due to the size and placement of the current group of MPAs. However, their overall benefit is likely to be too small to offset the scale of major thermal events. MPAs are clearly an important tool in managing coral reef health, but they must be complemented with direct measures aimed at reducing the anthropogenic activities responsible for climate change.
Figure 4.1 Region delineations for the analysis. Boundaries for regions are based on biogeographic patterns in diversity and similar management. Purple dots represent reef locations.
Figure 4.2 Coefficient estimates for the multilevel model. The 95% credibility intervals (thin grey line) and the 50% credibility intervals (thick black line) as well as point estimates (median) of the posterior distributions for all parameters using a Bayesian approach to fit the model in Eqn. (4). There is a 95% probability that the true value lies within the 95% credibility interval. The MPA x 10-Year Trend term should be contrasted with the 10-Year Trend term, which is the trend for controls. The MPA x 10-Year Trend term is an effect and gets added to the 10-Year Trend term when MPA = 1 to obtain the trend for MPAs. The magnitude of the anomaly effect varies according to the number of anomalies in the 2 years preceding the live coral cover survey. The effect of 5 total anomalies is displayed.
Figure 4.3 The effect of TSA on logit coral cover for each spatial grouping unit split by MPA and non-MPA. The bottom edge of the box denotes the 1st quartile of the data, the top edge locates the 3rd quartile, and the horizontal line inside the box corresponds to the median. The mean values are represented by the red stars. Both unweighted and weighted (inverse of the standard error of the mean) T-tests based on the observations of the coefficients for MPAs versus non-MPAs in the figure were non-significant (p>.65). These results are consistent with the more accurate estimates from the multilevel model (p>.15; see text).
Figure 4.4 Multilevel model predictions of the effect of thermal stress anomalies (TSA) on the change in coral cover at (A) different levels of coral cover and anomaly frequencies and (B) when coral cover is 50%. The 95% credibility intervals (thin black line), 50% credibility intervals (thick grey line), and point estimates (median) of the posterior distributions are shown.
**Figure 4.5** Comparison of anomaly frequency within MPAs to anomaly frequency of all reefs. Variability by year in (A) mean anomaly frequency (open circles) and (B) standard deviation for the theoretical distribution of anomaly frequency for all reefs and its 95% confidence intervals (error bars). The mean MPA anomaly frequency and standard deviation (black star) are generally lower.
Figure 4.6 Anomaly sizes for different regions (Fig. 4.1). Bars represent the anomaly size at which 50% (black), 75% (white), 90% (grey), and 95% (hashed) of the sizes are included.
Acknowledgments

T. Kristiansen, M. O'Connor, P. Reynolds, and J. Weiss for helpful comments on the manuscript. The Great Barrier Reef Marine Park for the GIS data for the Great Barrier Reef zoning and The Nature Conservancy for MPA boundaries for the Caribbean.
References


Figure S1.1 Mean duration (weeks) of TSAs, 1985-2005 in (A) Indo-Pacific and (B) Caribbean.
Figure S1.2 Mean duration (weeks) of WSSTAs, 1985-2005 in (A) Indo-Pacific and (B) Caribbean.
Figure S1.3  Mean duration (weeks) of TSA in 1998 in (A) Indo-Pacific and (B) Caribbean.
Figure S1.4 Mean duration (weeks) of WSSTAs in 1998 in (A) Indo-Pacific and (B) Caribbean.
Table S1.1 Validations of the CoRTAD data using \textit{in situ} data loggers at different depths and locations. Data presented included mean diff. (the mean difference between the logger data and the satellite data), RMS (root mean square), N (number of observations) and $r^2$. Logger data come from the Perry Institute for Marine Science (Bahamas), the National Data Buoy Center (Florida Keys, Hawaii), Erich Bartels/MOTE Marine Laboratory (Florida Keys), Peter Edmunds (U.S. Virgin Islands), and the CRC Research Centre (Great Barrier Reef).

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APPENDIX 2
Supplementary material for Chapter 3

2.1 Levels of management

There is no direct measure of management effectiveness in the MPA database, but all of the MPAs have an assigned World Conservation Union (IUCN) category. These categories reflect management objectives, but do not have specific criteria associated with them. Categories I-IV are generally accepted as protected areas in the traditional sense that they are protecting an ecosystem and permit only active restoration or population control, although permitted recreational and commercial fishing may be allowed (The World Conservation Union (IUCN) & World Commission on Protected Areas 2000). More controversy has developed about the final two categories, V and VI. Their stated purposes are to protect cultural values and sustainable use, respectively (The World Conservation Union (IUCN) & World Commission on Protected Areas 2000). These categories have been criticized as pushing the boundaries of what defines a protected area. Locke & Dearden (2005) propose reclassifying V and VI as sustainable development areas.

2.2 Logistic-normal distribution

Percent coral cover is a limited range response variable, because it is constrained to lie between the limits of 0 and 100 (Long 1997). Our dataset spans the range from near 0 to
100. Such a wide range of data can pose problems for ordinary linear regression particularly when the response variable lies near one of the boundaries. These problems persist with a log transform because the lognormal distribution is unbounded above. Standard solutions involve transforming the response (logit or arcsine) or choosing a probability model (beta) that constrains the response to lie within its natural limits. We chose a logit transform based on AIC comparisons with these other approaches.

2.3 Distance pairing

In this study, we used the distance to the nearest MPA to create spatial structure units for the non-MPA surveys, which we then used as a level 3 structural variable in the model. This definition exercise is analogous to trying to identify the appropriate blocking unit to which "treatments" (MPA versus non-MPA) are applied in an ANOVA context. There are currently no studies examining what an appropriate distance is for pairing MPA and non-MPAs surveys to determine differences in their effects on coral cover. Several studies have analyzed within MPA effects and quantified spillover into adjacent areas (McClanahan & Mangi 2000; Roberts et al. 2001; Abesamis & Russ 2005). However, for this analysis we were trying to pair protected and non-protected areas of relative homogeneity rather than establish the spatial extent of MPA effect. For all non-MPA surveys, we calculated the distance to the nearest MPA boundary that included a survey.

We then used maximum likelihood estimation to assess how changing the pairing distance influenced the MPA effect on slope. Without theory to motivate a distance threshold cut-off, we used a maximum likelihood approach to objectively select a distance cut-off. We ran our model pairing data at 13 different distances ranging from 1 km to 4000
km. At a distance of zero, each spatial unit or block had a single treatment, MPA. When the
distance was greater than zero, non-MPA surveys were added to the spatial unit or block.
Non-MPA surveys that were not close enough to be paired with an MPA area were assigned
to their own spatial unit. We would expect that by increasing block size a treatment effect
would become easier to detect in part due to the greater power achieved by a larger sample
size. On the other hand, increasing the size of the spatial unit could increase variability
within the block by adding dissimilar areas. These features suggest that there should be some
optimal choice for distance pairing. The shape of our loglikelihood curve was concave down
(Fig. S1) with a well-defined maximum, indicating that there was indeed an optimal value.
We found that the loglikelihood was maximized at 200 km, indicating that a model that used
200 km as a distance cut-off for pairing was relatively better than the other models examined.
In addition, this cut-off allowed more than 60% of non-MPA surveys to be assigned to spatial
structural units with MPA surveys.

2.4 Bayesian fitting

All final models were refit as Bayesian models using Markov chain Monte Carlo (MCMC) to
obtain more realistic estimates of parameter precision. For the MPA versus non-MPA
model, uninformative priors were taken for all model parameters. For the MPA only model,
a slightly informative prior was used for the breakpoint to bound the Markov chains away
from zero. Three separate chains were run and mixing was assessed both graphically and
analytically. Iterations were continued until all parameters yielded $\hat{R}$ values (the square root
of the variance of the mixture of all chains divided by the average within chain variance) that
were less than 1.1 for all parameters. The first half of each chain was discarded as a burn-in period and the remainder was thinned to minimize serial correlations.
Figure S2.1 The relationship between the MPA effect on slope and the distance of non-MPAs surveys from MPAs. The loglikelihood (solid black line) is maximized at 200 km, where approximately 60% of the non-MPA data has been paired in a structural unit with MPA data (dashed green line). MPA effect on slope and confidence intervals (grey dashed line) do not vary significantly with distance.
Figure S2.2  AIC values for all models examined. The best model is the one with the smallest AIC value. In this case, the best model is one in which MPA modifies the slope and intercept and ocean modifies the intercept only. Models with AICs that exceed 18650 are designated with arrows.
Figure S2.3  Coral cover slope and intercept values from the MPA versus non-MPA model. (A) The change in percent coral cover per year inside and outside of MPAs from 1996 to 1997 and a static estimate of (B) percent coral cover in 1996 with the 95% credibility intervals (thin grey line) and the 50% credibility intervals (thick black line) as well as point estimates (median) of the posterior distributions. Coral cover in MPAs may be lower than non-MPAs due to biases in their placement. By 2005, those differences disappear. Percent coral cover was obtained by back-transforming the predicted logit from the model.
Figure S2.4 Caterpillar plots for (A) the slope random effects and (B) intercept random effects for the level-3 residuals. Each point and associated vertical line in the plot represents the random effect for one spatial structural unit with paired protected and unprotected reefs (n=357) and its 95% credibility interval. Lines whose credibility intervals do not intersect the blue dashed line at zero are considered outliers of the model. The level-3 slope random effects are well-behaved. Only 4.2% of the data have an obvious indication of bad fit. By chance you would expect 5% of the data to lie outside 95% confidence intervals. The model does not describe level 3 intercepts as well, with 9.8% of the intercept random effects being outliers. At level 2, 0.7% of the slope random effects are outliers and 10.7% of the intercept random effects are outliers (not shown).
Figure S2.5 The number of reefs categorized by the year when their respective MPAs were established in the (A) Caribbean and (B) Indo-Pacific.
Figure S2.6 Times series of the number of years of protection by reef in the (A) Caribbean and (B) Indo-Pacific. Each grey line represents a single reef and shows the number of years of protection at the first survey and how that reef continued to be surveyed through time. A grey dashed line appears every 20 reefs. Gaps in the survey years can be seen by white breaks between the grey lines. The Caribbean had more reefs that had been protected for between 5-15 years and another group which had been surveyed at between 20-35 years of protection. The Indo-Pacific had a more even distribution across years, although there were fewer surveys in early years of protection.
Figure S2.7  Distribution of years protected by ocean

Pacific
n = 680

Indian
n = 86

Caribbean
n = 574

Years Protected
Figure S2.8 Generalized additive models for the (A) Caribbean and (B) Indo-Pacific. There is no evidence of a changepoint in the Caribbean, but there is in the Indo-Pacific.
Table S2.1 Percent of reef area by IUCN category. Management objectives are defined by The World Conservation Union (IUCN) and the World Commission on Protected Areas (2000).

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<tr>
<th>IUCN category</th>
<th>Management objectives</th>
<th>Percent of total reef area in category</th>
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<tr>
<td>I</td>
<td>science or wilderness protection</td>
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<tr>
<td>II</td>
<td>ecosystem protection and recreation (e.g. national park)</td>
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<tr>
<td>III</td>
<td>conservation of specific natural features (e.g. natural monument)</td>
<td>0.1</td>
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<tr>
<td>IV</td>
<td>conservation through management intervention</td>
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<td>V</td>
<td>landscape/seascape conservation and recreation (i.e. cultural values)</td>
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<td>VI</td>
<td>sustainable use of natural ecosystems</td>
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Table S2.2 List of models analyzed. The best model is the one with the smallest AIC value. In this case, the best model is one in which we have slopes and intercepts at levels 2 and 3.

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Table S2.3  Distribution of IUCN categories across oceans by surveys.

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Table S2.4  Distribution of IUCN categories across oceans by reefs.

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The World Conservation Union (IUCN) & World Commission on Protected Areas (2000). Protected areas: benefits beyond boundaries. In. International Union for Conservation of Nature and Natural Resources (IUCN) and the World Commission on Protected Areas Gland, Switzerland.