Title

Century-scale Records of Coral Growth and Water Quality from the Mesoamerican Reef Reveal Increasing Anthropogenic Stress and Decreasing Coral Resilience

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Century-scale records of coral growth and water quality from the Mesoamerican Reef reveal increasing anthropogenic stress and decreasing coral resilience

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in
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by
Jessica Elizabeth Carilli

Committee in charge:

Professor Richard Norris, Chair
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2009

The dissertation of Jessica Elizabeth Carilli is approved, and it is acceptable

in the quality and form for publication on microfilm:

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I doubt any PhD dissertation could be completed without extensive support and assistance from a large crowd of people, and this one is no exception. In somewhat chronological order, here goes. My parents, of course, were there first, and have always been incredibly supportive of my endeavors. At times they have believed in my abilities much more than I have, and that has gotten me through so much. Cynthia and Jim, Brian and Mary, I love you dearly. Thanks to my siblings: Mark, Patrick, Sam, and Annie, for helping make me who I am. I've been trying to set a good big-sister example and that's also gotten me through all of this. Thanks also to Mark for being an excellent field assistant; especially for snorkeling under the pier with me at 4 am to collect our shortly-lived coral nubbins.

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MATERIAL SUBMITTED FOR PUBLICATION IN THE DISSERTATION

Chapter 2 was accepted for publication to PLoS ONE as: Carilli, Jessica; Norris, Richard D; Black, Bryan; Walsh, Sheila W; McField, Melanie. “Local Stressors Reduce Coral Resilience to Bleaching.” The dissertation author was the primary investigator and author of this paper.

Chapter 3 was submitted for publication to Global Change Biology as: Carilli, Jessica; Norris, Richard D; Black, Bryan; Walsh, Sheila W; McField, Melanie. “Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold.” The dissertation author was the primary investigator and author of this paper.

Chapter 4 was submitted for publication to Marine Ecology Progress Series as: Carilli, Jessica E; Godfrey, Jessie; Norris, Richard D; Sandin, Stuart A; Smith, Jennifer E. “Periodic endolithic algal blooms in *Montastraea faveolata* corals represent periods of low-level stress.” The dissertation author was the primary investigator and author of this paper.

Chapter 5 was submitted for publication to Marine Pollution Bulletin as: Carilli, Jessica E; Prouty, Nancy G; Hughen, Konrad A; Norris, Richard D. “Century-scale records of land-based activities recorded in Mesoamerican coral cores.” The dissertation author was the primary investigator and author of this paper.

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Carilli J, Norris RD, Black B, Walsh S, McField M. Local stressors reduce coral resilience to bleaching. *In press,* PLoS ONE.

Carilli J, Norris RD, Black B, Walsh S, McField M. Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. *In press,* Global Change Biology.

Carilli J, Prouty NG, Hughen K, Norris RD. Century-scale records of land-based activities recorded in Mesoamerican coral cores. *In press,* Marine Pollution Bulletin.

Carilli J, Godfrey J, Norris RD, Smith J, Sandin S. Green bands in *Montrastraea faveolata* corals are proxies for past stress. *In review*, Marine Ecology Progress Series.

Saenger C, Cohen AL, Oppo DW, Halley RB, **Carilli JE**. Low-latitude north Atlantic sea surface temperature trends and variability since 1552. *In press,* Nature Geoscience.

Hartmann A, **Carilli J**, Norris RD, Charles CD. Stable isotopic records of bleaching and endolithic algae blooms in the skeleton of the boulder forming coral *Montastraea faveolata*. *In prep.*

Koenig A, **Carilli J**, Buster N. A comparison of chemical records in *Montastraea faveolata* and *Siderastrea siderea* as examined by laser ablation ICP-MS: A look at methodology for Caribbean coral for seasonal and storm events. *In prep.*

Fields of Study

- Coral reef ecology
- Sclerochronology
- Human impacts on marine systems
- Coral bleaching
- Trace metal geochemistry
- Isotope geochemistry

ABSTRACT OF THE DISSERTATION

Century-scale records of coral health and water quality from the Mesoamerican Reef reveal increasing anthropogenic stress and decreasing coral resilience

by

Jessica Elizabeth Carilli

Doctor of Philosophy in Earth Sciences

University of California, San Diego, 2009

Professor Richard Norris, Chair

Coral reefs provide extensive ecosystem goods and services to the communities that depend upon them including food, shoreline protection, and tourism income. Unfortunately, reefs worldwide are being devastated by a range of factors including overexploitation, pollution, and ocean warming and acidification. This study was undertaken with a conservation-minded focus: I wanted to investigate why reefs in Mesoamerica were dying, in order to inform management decisions regarding resource allocation for reef protection. I suspected that runoff was a major impact in the region that was not being taken into account. While the establishment of marine protected areas is important, these boundaries do not prevent polluted runoff from reaching the reefs.

In order to investigate whether runoff was negatively impacting the reef, I collected numerous core samples from large *Montastraea faveolata* coral heads. I measured coral growth rates, metal content, and stable carbon and oxygen isotopes in order to reconstruct changes in coral health and water quality, respectively. I found that the site with the highest levels of runoff had a decreasing trend in extension rates beginning in the 1970's, indicating that as runoff has increased, coral growth has begun a slow decline. There was no long-term decline at other sites, but all sites were severely impacted by bleaching in 1998. Bleaching (the loss of the coral's symbiotic algae) on this large of a scale is caused by thermal stress. I investigated long-term records of heat stress, and found that 1998 was not an exceptional year: 1958 was even warmer in this region, yet no bleaching had occurred, as indicated by a lack of skeletal growth anomalies. This might be explained by a reduction in the coral's thermal tolerance threshold in recent years, and I hypothesize that local anthropogenic stress is the culprit. I also found that coral growth rates did not recover, even 8 years after the bleaching event, at sites that experience higher local stress, quantified here using a combination of local human population, fish abundance, sedimentation, and nutrient runoff. These findings indicate that coral resistance to bleaching and resilience after bleaching (as quantified by growth rates) are both reduced with local stress is high.

CHAPTER 1: Introduction

INTRODUCTION

Coral reefs are among the world's most productive and diverse ecosystems (Reaka-Kudla 1997). Unfortunately, they are being lost at an alarming rate; Gardner et al. (2003) estimated that on average, live coral cover had declined by 80% in the Caribbean in 30 years. This recent abrupt loss of corals can be attributed to several human-induced impacts. These include overgrowth by fleshy macroalgae, whether due to algal growth stimulation from nutrient pollution and/or a reduction in herbivory due to overfishing (Hughes 1994, Lapointe 1997, McCook 1999, McCook et al. 2001, McClanahan et al. 2003, Smith et al. 2006); abrupt smothering or a slow reduction in fitness due to sedimentation (Dodge and Vaisnys 1977, Rogers 1990, Reigl and Branch 1995, Fabricius and Wolanski 2000); direct damage due to destructive fishing practices (McManus et al. 1997), irresponsible tourism (Barker and Roberts 2004), and boat damage (Saphier and Hoffmann 2005); and recent expansions in coral diseases (Harvell et al. 1999, Bruno et al. 2007). However, potentially the most alarming is coral bleaching, during which corals lose the symbiotic dinoflagellate zooxanthellae algae that provide most of their food, usually associated with unusually high thermal stress (Brown 1997). Coral bleaching appears to be increasing in frequency and geographic extent as the climate warms (Hoegh-Guldberg 1999, Hughes et al. 2003), and some major bleaching episodes have led to mass mortality; for instance after a mass bleaching event in 1998, almost all *Agaricia spp.* corals died in the Belize lagoon, which had been the dominant species (Aronson et al. 2002).

Interestingly, prior to *Agaricia* dominance, *Acropora spp.* were dominant in the lagoon, but were wiped out by disease in the 1980's (Aronson and Precht 1997).

Although coral loss appears to have occurred recently, underwater observation only began mid-century with the advent of SCUBA diving, and rigorous ecological research began even more recently. Although some human impacts such as land-based runoff are considered a recent phenomenon, humans have been affecting reef environments for much longer, mainly through fishing. For instance, Pandolfi et al. (2003) compiled records showing that in some places, reef degradation began centuries ago. However the Mesoamerican Reef, specifically the Belizean portion, was considered to be relatively pristine until the 20th century (Arrivillaga and Garcia 2004).

I decided to investigate records of coral growth from skeletal cores in order to determine whether recent catastrophic losses of corals in Mesoamerica were preceded by reductions in coral growth rates, and whether the timing of this reduction coincided with increases in land-based runoff as measured by geochemical analysis of the coral cores. Shinn (1966) found that coral growth rates were reduced in unfavorable conditions in terms of water temperature, while Dodge and Vaisnys (1977) found that corals exposed to sedimentation stress grew more slowly, presumably because more energy was allocated to sloughing off sediment that skeletal growth. Hudson et al. (1976) discussed the use of sclerochronology as a way to investigate past environmental and ecological change, and Hudson (1981, 1985) and Hudson et al. (1989, 1994) interpreted changes in coral growth rates in the context of stressors including dredging operations, nuclear bomb testing, railroad construction, extreme weather, and nutrient runoff. Dodge and Lang (1983) found that growth rates in *Montastraea annularis* at the Flower Garden Banks were well correlated with water temperature and river discharge rates. Lough and Barnes (1997, 2000) found that growth rates in corals from the Great Barrier Reef were well correlated with water temperatures, and they pointed out that deviations from this correlation could indicate unnatural change. More recently, Halley and Hudson (2007) investigate the frequency of anomalous coral growth associated with bleaching and found that coral bleaching in Florida appears to be a recent phenomenon. Guzman et al. (2008) investigated coral growth rates near the Panama Canal and found long-term reductions in growth rates since the canal was constructed.

Although I found a steady increase in geochemical runoff indicators, instead of a corresponding gradual decline in coral health, I found almost no change until massive and abrupt growth declines due to the 1998 mass bleaching event. I also found significant differences in recovery after the bleaching event for corals experiencing differing levels of background stress. I interpret these observations as indicating that local background stress and climate change interacted synergistically to pass the coral's tolerance threshold, as hypothesized by Knowlton and Jackson (2008). Corals had been able to resist the negative effects of warm water temperatures earlier in the century when local stress was low, and before 1998, corals were able to cope with local stress; the combination, however, may be the explanation for the devastation caused by the 1998 mass bleaching event.

For this dissertation, I collected numerous skeletal cores from a small area at each of my four sites. I analyzed annual skeletal extension rates, density, and calcification, and used tree-ring statistical techniques to cross-date all of the records, produce master chronologies of growth at each site, and estimate the integrity of the growth signals at each site. I investigated both long-term changes in coral growth rates as well as recovery of growth rates after a major bleaching event. I studied recurring episodes of high populations of endolithic algae in the coral skeleton and hypothesize that they are caused by periods of low-level coral bleaching. I also reconstructed long-term records of land-based runoff onto the reef using metal/Ca ratios measured on skeletal samples. In addition, I constructed approximately bi-monthly scale records of carbon and oxygen isotopes at each site, which may be useful for investigating the main climatic influences in the region.

CORAL BLEACHING

Coral bleaching is a generalized response to stress in which the coral’s symbiotic zooxanthellae are expelled or consumed (Fitt et al. 2001). Coral bleaching occurs as a response to stress, and has been shown to occur in response to low salinities (Goreau 1964), cold temperatures (Muscatine et al. 1991) and high and low light (Glynn 1996), and other factors but on a large scale the most common cause for bleaching is thermal stress (Fitt et al. 2001). Thermal stress causes the zooxanthellae photosystem II to breakdown and produce reactive oxygen species (Lesser 1997, Downs et al. 2002). The coral host must then expel its zooxanthellae to avoid cellular damage by oxidative stress.

Corals are found in locations around the world that experience a wide range of mean temperatures, and some species have ranges that span a vast difference in thermal regimes (Hughes et al. 2003). The corals in each location appear to be adapted to their local thermal regimes, and a 1°C increase above the mean maximum monthly temperature will often result in bleaching (Hoegh-Guldberg 1999). However, there are many reasons that this thermal tolerance threshold is probably not static. Different clades of zooxanthellae have been shown to have different levels of thermal tolerance (Rowan et al. 1997, Berkelmans and van Oppen 2006, Garren et al. 2006) and corals may be able to shift or shuffle their symbionts as one way to resist future bleaching (Baker et al. 2004, Rowan 2004, Berkelmans and van Oppen 2006). Beyond this, other physiological and environmental effects beyond temperature can affect a coral’s ability to withstand or recover from bleaching. Rodrigues and Grottoli (2007) showed that corals with higher lipid content before bleaching survived better than those with lower original lipid stores, Salih et al. (2000) found that fluorescent proteins in corals are photoprotective and can increase coral resistance to bleaching during heat stress, and there may be other as yet unrecognized physiological responses as well (Hughes et al. 2003). There is also some evidence, including that presented in chapter 3 of this dissertation, that local stress such as poor water quality can reduce the thermal tolerance of corals (Wooldridge et al. 2009).

Although there may be no simple thermal threshold at which corals bleach, it is still important to compare how corals respond to changes in thermal and other forms of stress. To quantify thermal stress experienced by corals, several approaches have been taken. These include calculating “hotspots,” or locations in which the sea surface temperature (SST) exceeds 1°C above long-term average high temperatures (Goreau and Hayes 1994), “degree-heating-weeks,” or rolling 12-week windows that sum up all hotspot values (Strong et al. 1997), “degree-heating-months,” which draws from monthly SST data (Lough 2000), and “max-3d,” or the highest 3-day summertime SST (Berkelmans et al. 2004). High spatial and temporal resolution SST data (Berkelmans et al. 2004, Weeks et al. 2008) and reef topography data (Wooldridge and Done 2004) can more accurately predict bleaching than coarser-scale SST data, but these high resolution data are not available over long time periods. Therefore, for this dissertation work, the degree-heating-week and degree-heating-month methods were used to compare thermal stress between sites during 1998 and over time, respectively.

RESISTANCE AND RESILIENCE

Resistance and resilience are concepts that have different meanings for different researchers (West and Salm 2003, Bellwood et al. 2004), but here I use resistance in the sense described above: that a coral has a certain level of stress it can tolerate (or threshold) before it responds by bleaching and/or changing its growth rate. I use the term resilience to describe the ability of a coral animal to recover back to normal growth once a stress is removed, but on an ecosystem scale, resilience can also refer to the ability of a coral reef to remain coral-dominated (Bellwood et al. 2004, Knowlton 2004). On coral reefs, a large amount of research has focused on finding the cause of reef degradation and specifically the reasons that reef resistance and resilience are eroded, in order to effectively manage reefs for the future. The resulting conclusions can generally be split into two groups: those that attribute degradation to very recent events such as disease and bleaching, and those that posit that reef resistance and resilience were undermined long ago, paving the way for these recent shocks to cause widespread damage. In the first scenario, reefs are experiencing new and lethal stressors in the form of coral disease and bleaching (Aronson et al. 2003, Aronson et al. 2005, Aronson and Precht 2006). Conversely, under the second scenario, as human-induced stressors like fishing and land-based pollution increase over time, reef resistance and resilience are being slowly eroded, such that a sudden, but not necessarily novel, shock can send reefs over a threshold of sudden decline (Scheffer et al. 2001, Pandolfi et al. 2003, Hughes et al. 2003, Knowlton 2004, Mumby et al. 2007, Knowlton and Jackson 2008). In this dissertation I discuss how local stress, quantified using a combination of local human population, fishing pressure, sedimentation, and nutrient runoff interact with thermal stress to undermine coral resistance and resilience, defined in relation to coral growth rates.

STUDY LOCATION

The Mesoamerican Reef is the second-largest barrier reef in the world, and is located in the western Caribbean Sea, offshore from Mexico, Belize, Guatemala, and

Honduras (Fig. 1-1). The reef lies close to shore off of Mexico, but increases in distance from shore moving south into Belize, forming a barrier reef with numerous small patch reefs and cayes in the lagoon between the mainland and the reef edge. There are also several offshore “atolls,” which have small sand cayes surrounding a central lagoon but were not formed by subsiding volcanoes so are not true atolls. The reefs in Honduras are less extensive and mostly confined to areas surrounding the Bay Islands and Cayos Cochinos (Kramer et al. 2000). On the deep fore-reef, spur-and-groove formations that are dominated by *Montastraea faveolata* are common (Fig. 1-2; McField 2000), and this study was restricted to those habitats in order to reduce the number of factors potentially affecting my results.

Rainfall and associated runoff in the region is concentrated in the south, where high mountains surround the Gulf of Honduras (Fig. 1-3; Thattai et al. 2003, Burke and Sugg 2006). Circulation around the reef has been a focus of several recent studies. These all indicate that the region is dominated by a counter-clockwise gyre that spins off the main northwesterly-flowing Caribbean current, and that there is significant connectivity between river runoff and the reef system (Tang et al. 2006, Heyman and Kjerfve 1999, Chérubin et al. 2008, Paris and Chérubin 2008, Soto et al. 2009). I chose sites expected to experience a gradient of land-based runoff in order to compare the relative impacts of runoff between sites: Turneffe Atoll in the north with the least continental influence, Sapodilla Cayes with the most, Cayos Cochinos the second-most, and Utila the third-most (Fig. 1-1). Indeed, metal/Ca ratios measured in replicate samples from the top 5 years of multiple coral cores from each site confirmed this relative pattern of continental influence (Prouty et al. 2008).

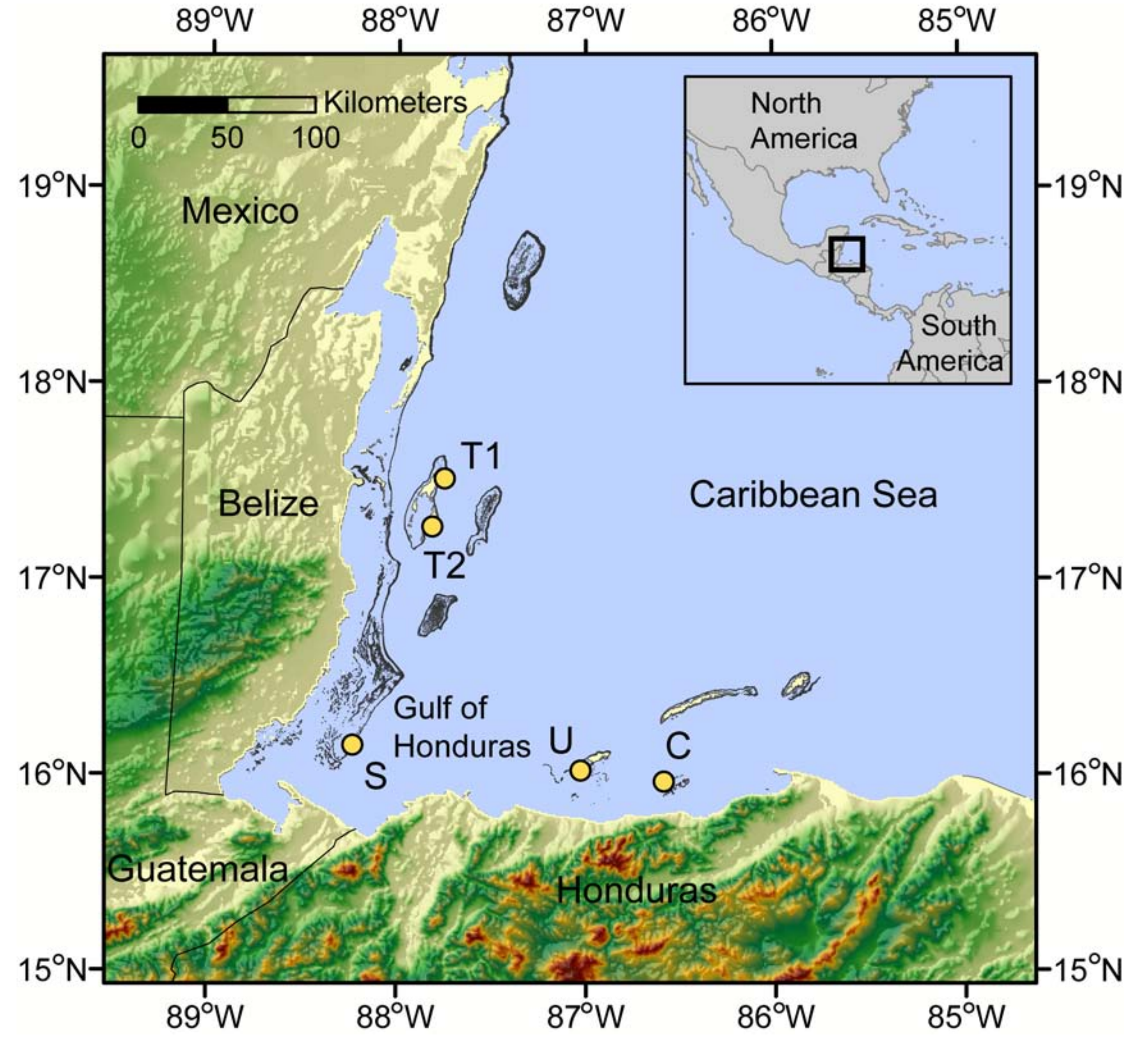

Figure 1-1. Map of the Mesoamerican Reef and surrounding region. Reef is in dark gray; sites are shown as yellow circles. T1, T2 = Turneffe Atoll sites, S = Sapodilla Cayes, U = Utila, C = Cayos Cochinos. Surrounding land shows topography, with greens and warm colors higher than tan coloring.

Figure 1-2. Typical spur-and-groove habitat on the deep fore-reef. Spurs are dominated by *Montastraea faveolata*. Spurs and grooves, or sand channels, are aligned in an onshore-offshore orientation. Photo by Konrad Hughen.

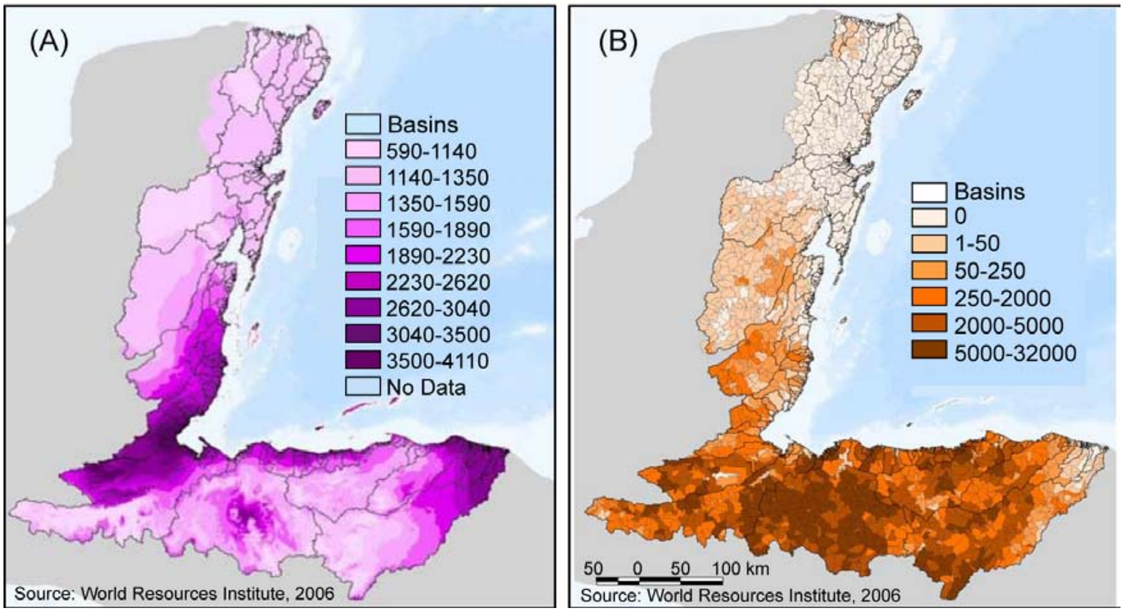

Figure 1-3. Watersheds draining onto the Mesoamerican Reef with: (A) annual rainfall in mm (B) annual sediment erosion in meters/km^2. Both of these images are modified from Burke and Sugg (2006).

CORAL CORE COLLECTION

I collected cores (a total of 92, 14 from Cayos Cochinos, 17 from Utila and Turneffe, and 44 from the Sapodilla Cayes) using SCUBA and a hand-held reversible air drill (Ingersoll-Rand 7803RA, 500 rpm) driven by a gas-powered air compressor (Westward 4B220, 10 cfm) (Fig. 1-4). A custom-built stainless steel core barrel 6 cm in diameter and 50 cm long fitted with a brass drill head containing carbide teeth was fashioned after the design developed by the Australian Institute for Marine Science (Fig. 1-5). After core removal, pre-cast concrete plugs were inserted to prevent colonization inside the coral by boring organisms and allow coral regrowth (Fig. 1-6). Surveys at later dates confirmed that regrowth was occurring (Fig. 1-6). At each site, the boat was moored or anchored in a sand channel, and I collected cores from the largest heads within reach of a 100-foot-long hose. Cores were drilled vertically to obtain the clearest banding pattern along the maximum growth axis.

After collection, tissue was removed using a waterpik and the cores were rinsed in fresh water and air-dried. A ~0.86 cm thick slab from the middle of each core was cut using a water-lubricated double-bladed diamond table saw. Finally, core slabs were cleaned in de-ionized water and then air-dried. Core slabs were x-rayed at UCSD Thornton Hospital using a Siemens Polyphos 50 with a source-to-object distance of 40 inches and a setting of 63 kilovolts at 5 milliamps/second. Digital x-ray cassettes were processed using an AGFA Musica ADC Compact Plus, and images saved in DICOM format, as well as hard copy films.

Figure 1-4. Drilling a coral core in Belize. Photo by Brad Erisman.

Figure 1-5. Core barrel. One carbide tooth is missing.

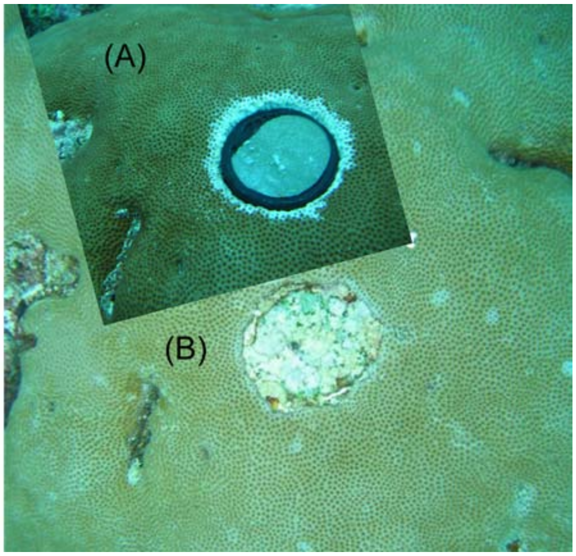

Figure 1-6. Core holes with concrete plugs. (A) Freshly plugged hole and (B) the same hole one year later. Note that this is a *Siderastraea siderea* coral head. Photo B taken by Polly Wood.

OUTLINE OF THE DISSERTATION

The remainder of this dissertation consists of six chapters. In chapter 2, I quantify the relative human impacts at each of my four sites, and investigate the recovery of coral growth rates after the 1998 bleaching event given these differing levels of background impacts. Not only were corals with lower levels of local stress more resilient to bleaching, but there is also evidence for higher resistance as well. These results indicate that there is a synergistic impact between background local stress such as overfishing and runoff and large-scale global heat stress associated with climate change. Chapter 3 builds on this concept, and shows that while the 1998 bleaching event was unprecedented in its severity, heat stress in 1998 was not exceptional. This indicates that the reason coral bleaching in 1998 was so severe on the Mesoamerican Reef may have been that local background stress lowered the coral thermal tolerance, and caused bleaching even at temperatures that were not particularly extreme. Chapter 3 also discusses in detail the tree-ring statistics that were used to construct the growth rate chronologies used in both chapter 2 and 3.

Chapter 4 discusses the incidence of periodic large populations of endolithic algae of the genus *Ostreobium* that appear as green bands in the coral cores. Previous studies had hypothesized that these bands might be simply accumulations of algae due to slower coral growth. I find no relationship between coral growth rate and the incidence of green banding, and conclude that instead, these green bands are blooms of algae. I also find that the incidence of green banding increases over time, and hypothesize that the blooms occur due to coral paling (low-level bleaching), which is becoming more prevalent towards the present as human impacts increase.

In chapter 5, I show century-scale records of annually-resolved metal/Ca ratios of seven metals: Ba, Mn, Cu, Cr, Sb, Zn, and Pb, measured from one long core from each site. The long-term records hold constant the same patterns of continental influence over the length of the record, and Ba/Ca, which is used as a proxy for sedimentation, increases at all sites. This indicates that as human populations and development have expanded in the watersheds surrounding the Mesoamerican Reef, all sites have experienced an increase in the overall level of continental influence. In chapter 6, I investigate records of stable carbon and oxygen isotopes measured approximately bimonthly through about 70 years of core material from one core at each site. These records are compared the various climatic variables to explore the main drivers of variability in the region. In chapter 7, the major conclusions resulting from this work are summarized.

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CHAPTER 2: Local Stressors Reduce Coral Resilience to Bleaching

ABSTRACT

Coral bleaching, during which corals lose their symbiotic dinoflagellates, typically corresponds with periods of intense heat stress, and appears to be increasing in frequency and geographic extent as the climate warms. An important question in coral reef ecology is whether chronic local stress reduces coral resistance and resilience from episodic stress such as bleaching, or alternatively promotes acclimatization, potentially increasing resistance and resilience. Here I show that following a major bleaching event, *Montastraea faveolata* coral growth rates at sites with higher local anthropogenic stressors remained suppressed for at least 8 years, while coral growth rates at sites with lower stress recovered in 2-3 years. Instead of promoting acclimatization, my data indicate that background stress reduces coral fitness and resilience to episodic events. I also suggest that reducing chronic stress through local coral reef management efforts may increase coral resilience to global climate change.

INTRODUCTION

Ecological studies have demonstrated that stressors currently affecting coral reefs include, among others, coral disease (Harvell et al. 1999), overgrowth by fleshy macroalgae, whether due to algal growth stimulation from nutrient pollution and/or a reduction in herbivory due to overfishing (Hughes 1994, Lapointe 1997, McCook 1999, McCook et al. 2001, McClanahan et al. 2003, Smith et al. 2006), and abrupt smothering or a slow reduction in fitness due to sedimentation (Dodge and Vaisnys

1977, Rogers 1990, Reigl and Branch 1995, Fabricius and Wolanski 2000). These chronic stressors are often associated with the gradual loss of coral cover and overgrowth by fleshy algae. However, abrupt and severe episodic events, such as coral bleaching, may also be responsible for coral reef degradation (Knowlton 2001). An outstanding issue is whether the combination of multiple stressors reduces coral resistance or resilience to episodic events such as bleaching (Hughes et al. 2003, Knowlton and Jackson 2008, Sandin et al. 2008) or alternatively whether acclimatization to stressful conditions can increase coral resistance—the ability of corals to withstand future stress (Brown et al. 2002, Castillo and Helmuth 2005). Bleaching is a generalized term for the loss of symbiotic dinoflagellate zooxanthellae or their pigments in scleractinian corals and is typically associated with sustained, unusually warm water temperatures (Hoegh-Guldberg 1999). Several studies have found that bleaching reduces skeletal growth in corals (Goreau and Macfarlane 1990, Leder et al. 2001, Suzuki et al. 2003). Ocean acidification may also reduce the ability of corals to calcify as normal; a recent study of corals from the Great Barrier Reef attributes a 14.2% decrease in calcification since 1990 to a combination of acidification and warming (De'ath et al. 2009). Here I define resistance as an individual coral's ability to continue normal skeletal growth even under stress (whether chronic or episodic), and resilience as a coral's ability to recover to normal growth rates after a stressful event (Fig. 2-1A-C). To test the hypothesis that chronic local stress reduces coral resistance and resilience to bleaching, I focus on coral growth before and after the 1998 mass-bleaching event (Kramer et al. 2000) from four sites on the Mesoamerican Reef (Fig. 2-2, Table 2-1) with relatively high and low chronic local stress.

Table 2-1. Coral core collection site locations. Location names with dive site name or nearby caye, coordinates, number of cores from each site, along with growth anomalies in 1998 and earlier. Table lists the total number of cores which were drilled and slabbed along the growth axis, the percentage and number of these that have dense stress bands associated with the 1998 event, the percentage and number that contained a partial mortality scar, and any previous individual stress bands.

Site	**Dive Site Name**	**Coordinates**	**Total Cores**	**1998 Stress Band**	**Partial Mortality in 1998**	**Previous Stress Bands**
Turneffe 1	Dog Flea Caye	17°29’59”N, 87°45’30”W	17	71% (12)	6% (1)	2
Turneffe 2	Harry Jones	17°18’25”N, 87°48’04”W				
Sapodilla	Frank’s Caye, NE buoy	16°07’45”N, 88°14’59”W	44	100% (44)	16% (7)	0
Utila	Diamond Caye	16°03’52”N, 86°57’30”W	17	100% (17)	12% (2)	1
Cayos Cochinos	Pelican Point, Peli 2	15°58’41”N, 86°29’06”W	14	100% (14)	21% (3)	0
		Total	**92**	**95% (87)**	**14% (13)**	**3**

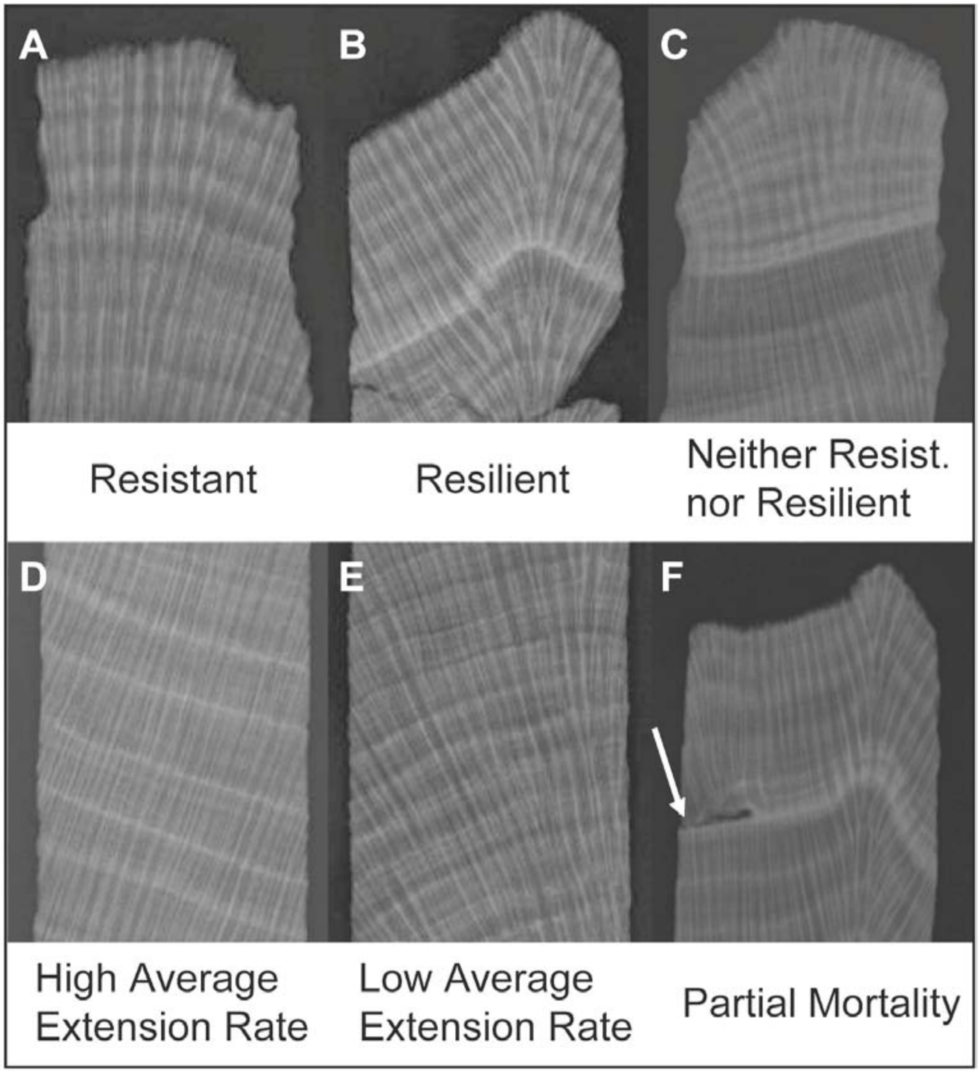

Figure 2-1. X-radiographs of various coral cores showing the different types of growth behavior discussed. (A) Coral without the 1998 growth suppression, indicating resistance to bleaching in 1998. (B) Coral with the 1998 growth suppression, recognized by the bright high-density band, but with a quick return to pre-1998 extension rates, indicating resilience after bleaching. (C) Coral with the 1998 growth suppression and continuing depressed extension rates after 1998, indicating a lack of both resistance and resilience to bleaching. (D) A coral with relatively high average extension rate. (E) A coral with relatively low average extension rate. (F) A coral with a partial mortality scar on the left (noted by white arrow), coincident with the 1998 growth anomaly.

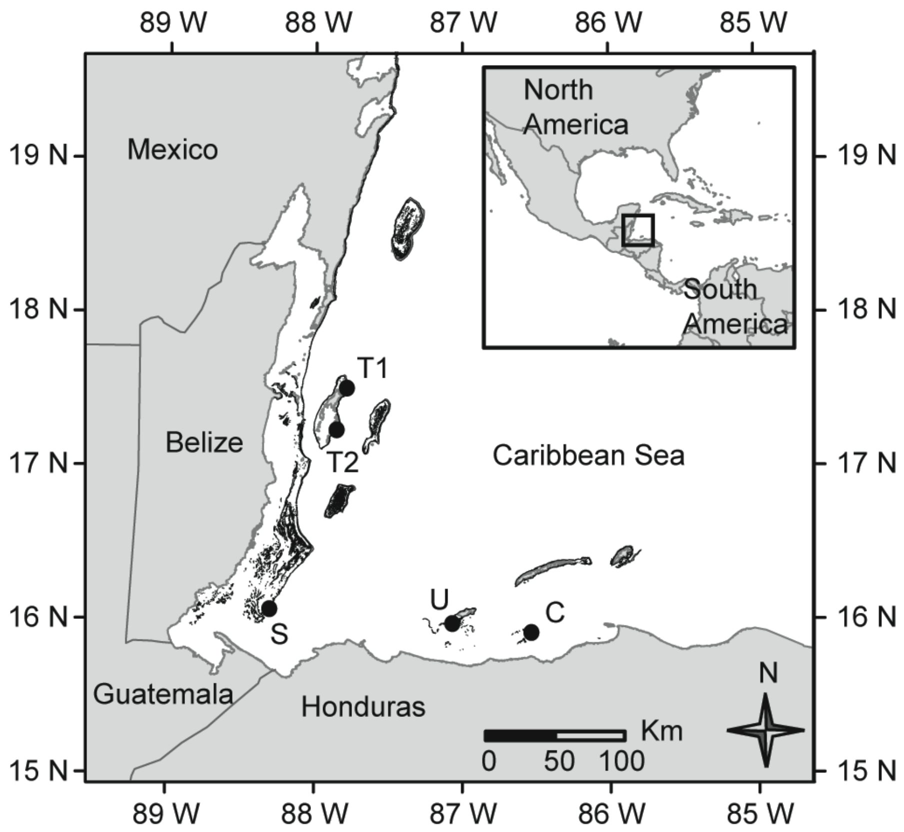

Figure 2-2. Map of the Mesoamerican Reef with locations of coral collections as black circles. Dark gray denotes coral, light gray denotes land areas. T1, T2 = Turneffe Atoll (4 cores from T1, 13 from T2), S = Sapodilla Cayes (44 cores), U = Utila (17 cores), C = Cayos Cochinos (14 cores).

METHODS

The level of local stress at each site was calculated using the methodology of Halpern et al. (2008) to estimate a cumulative impact index based on weighted, log-transformed, re-scaled data representing (1) sedimentation (2) nutrient input (3) local human population size adjacent to these sites and (4) a relative measure of fishing pressure based on fish abundance surveys (Healthy Reefs Initiative 2008, Supplement)

(Table 2-2). My calculated local impact scores for the Mesoamerican reef sites have the same ranking as the “Halpern Index” that I calculated as the average of 4 cells representing these sites from the Halpern et al. (2008) global impact map. I also compared my results with the integrated reef health index at these sites from the Healthy Reefs Report Card (Healthy Reefs Initiative 2008) (Table 2-2). According to all three indices of local stressors and reef health, my sites in the Sapodilla Cayes and Utila experience the highest levels of local stress, while sites in Cayos Cochinos and Turneffe Atoll experience lower levels.

I collected a total of 92 coral cores from *Montastraea faveolata*, the dominant reef-builder on the fore reef (McField 2000) between 2.5-13 m depth in spur and groove habitat (Table 2-1). Permission to collect and export coral samples was granted by the Belize Fisheries Department and the Secretaria de Agricultura y Ganadería, Honduras. Coral skeletal growth rates were measured based on annual density bands in the skeleton (Knutson et al. 1972, Cruz-Piñon et al. 2003, Supplement). Coral extension, average density, and calcification (the product of extension and density) were analyzed from digital x-rays using the program CoralXDS (Helmle et al. 2002) for each high-density, low-density annual couplet, though in this paper I focus on extension rates (cm/year). To ensure all growth-increment chronologies were annually resolved, I made novel use of tree-ring techniques, including “crossdating” of annual extension rate (growth-increment width), which uses comparisons of the growth records from each individual core to all others to check whether any rings were potentially mis-dated. Average extension rates and 95% confidence intervals were calculated using 10,000 bootstrapped samples from all cores from a site for each individual year (Fig. 2-3). Differences between sites were compared using pairwise permutation tests on extension rates between 1950-1997. Edinger et al. (2000) found that comparing absolute extension rates between sites is not necessarily representative of overall reef health. Indeed, Turneffe Atoll, one of the less impacted sites, has significantly ($p<0.001$) higher extension rates than the other three sites before 1998, but this site also lost significant coral cover due to the 1998 bleaching event and hurricane Mitch (Fig. 2-S1). Therefore, here I focus on resistance to and recovery after bleaching in 1998 instead of absolute differences between sites. Recovery to normal mean extension rates after 1998 were estimated, while controlling for the year, by fitting the generalized linear model (GLM): ($extension = \beta_0 + \beta_1 year + \beta_2 post1998$) (Table 2-S1). Extension rates from the years 1950 to 1997 (post1998=0) were compared to rates from 2002 to 2006 (post1998=1) to avoid the years 1998-2001 during which all sites had severely depressed growth.

Partial coral mortality has been empirically linked to the level of environmental stress on reefs in several locations (Guzman et al. 1994, Ruesink 1997, Nugues and Roberts 2003, Jordan-Dahlgren et al. 2005). I had originally intended to collect data on the frequency of partial mortality events seen in the coral cores; however there were no scars prior to those in 1998. Therefore, I was only able to compare the percentage of cores with and without a partial mortality scar in 1998.

Table 2-2. Anthropogenic stress scores. Four measures of local stress at each site: sedimentation, nutrients, human population and fishing pressure used to calculate my cumulative "Stress Index" (sources in supplemental information). A comparison with the Halpern et al. (2008) and Healthy Reefs Initiative (2008) indices is also shown, though note that only the relative rankings are comparable. Sapodilla and Utila experience higher local impacts and lower reef health. *Note that while low Stress Index and Halpern Index scores indicate fewer local stressors, a low Healthy Reefs Index score indicates worse reef health.

Site	**Sediment-ation**	**Nutrients**	**Human Population**	**Fishing Pressure**	**Stress Index**	**Halpern Index**	**Healthy Reefs Index***
Sapodilla	*1.60*	*1.80*	*0.00*	*0.00*	***3.40***	13.35	2.10
Utila	*0.91*	*0.56*	*2.30*	*-2.08*	***1.70***	13.27	2.49
Cayos Cochinos	*1.37*	*0.89*	*1.00*	*-2.41*	***0.84***	11.06	2.98
Turneffe	*0.00*	*0.00*	*0.31*	*-0.11*	***0.20***	9.80	2.59

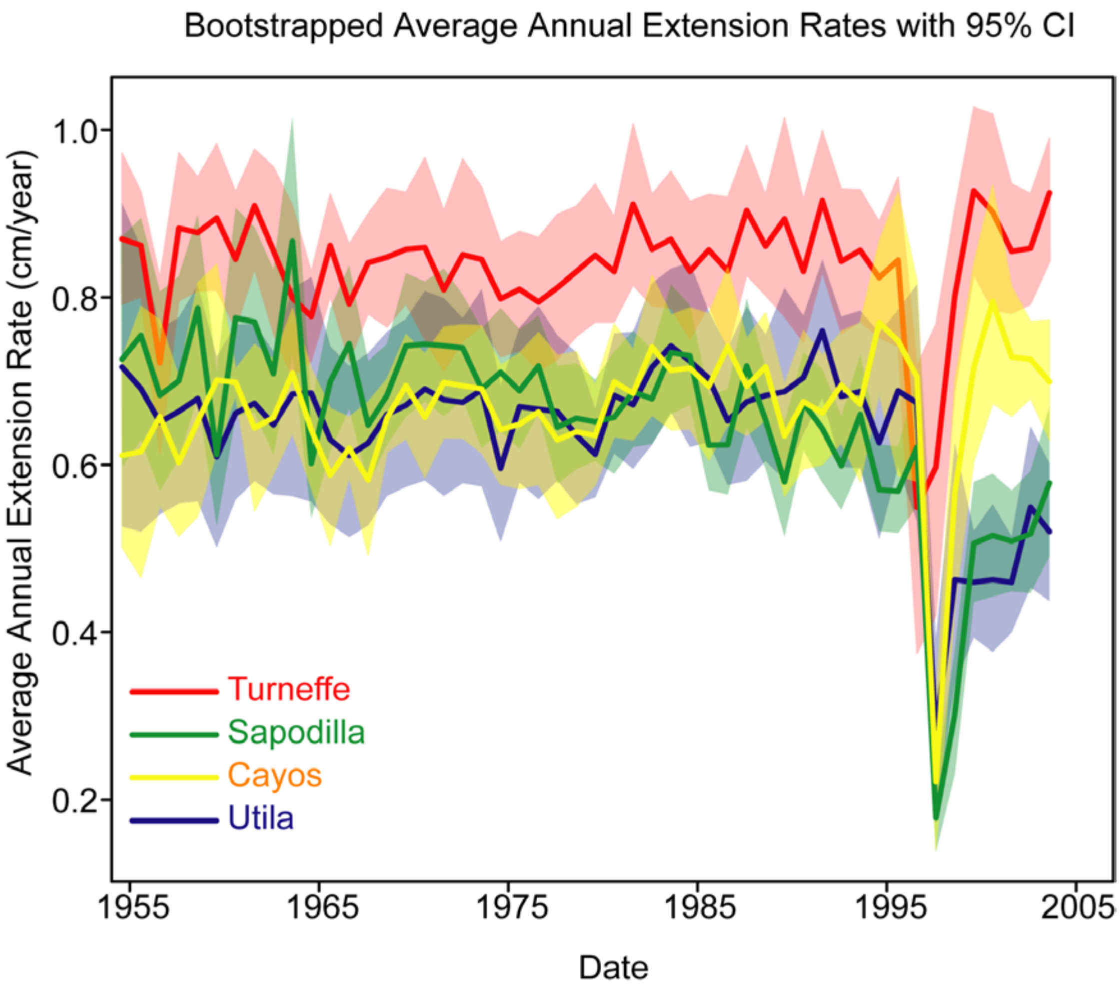

Figure 2-3. Bootstrapped means (solid lines) and 95% confidence intervals (shading) for extension rates after 1955. Extension rates at Sapodilla and Utila remain suppressed after the 1998 bleaching event (p<0.001).

RESULTS AND DISCUSSION

At all four sites, nearly every coral displays a visually prominent stress band (Leder et al. 1991) in 1998 (Fig. 2-1B), indicated by an increase in skeletal density and decrease in extension and calcification rates more than four standard deviations outside the mean chronology. Indeed, 95% of coral cores show a marked reduction in extension rates that persists for two years or more following the 1998 event (Fig. 2-3). Additional rare stress bands (denser than the long-term mean by at least 1.5 standard deviations) are seen in three individual coral cores in 1950, 1965 and 1995. However, no other coral cores displayed significant changes in growth during these years, nor did I observe any partial mortality scars before 1998.

Although the 1998 bleaching event affected the entire Mesoamerican reef system, there are spatial differences in its intensity revealed in my coral cores. I compared the number of coral cores with partial mortality scars (Fig. 2-1F) and 1998 stress banding between sites using a permutation test. Turneffe Atoll, the site with the lowest level of local stress, is also the only site without ubiquitous stress banding ($p<0.05$) (Fig. 2-1A), and has the lowest, but non-significant, frequency of partial mortality scars (Table 2-2). The lack of stress banding in some coral cores at Turneffe Atoll suggests that at least some of those corals may have resisted bleaching. By comparison, the universal occurrence of stress banding at all other sites supports the hypothesis that high chronic stress decreases coral resistance to bleaching.

In contrast to the modest variability in resistance to the 1998 bleaching event, there are large differences in the resilience of corals between sites. At Sapodilla and Utila where stress indices are high, coral growth still did not recover completely by the time of collection more than eight years following the 1998 bleaching event, even controlling for long-term decreasing trends at these sites (GLM: Sapodilla, $F_{(2,50)}=20.70$, $p<0.001$, $R^2=0.45$; Utila, $F_{(2,50)}=18.26$, $p<0.001$, $R^2=0.42$, Table 2-S1). Such a long recovery period after bleaching is unprecedented in the literature, with most studies reporting growth suppression due to bleaching on the order of one year (Goreau and Macfarlane 1990, Leder et al. 1991, Suzuki et al. 2003) and the longest growth suppression reported for four years (Omata et al. 2006). In comparison, corals from lower-stress sites (Turneffe and Cayos Cochinos) recovered to pre-bleaching extension rates in about three years (Fig. 2-3, Table 2-S1). However, at sites with high local stress, corals have been unable to recover to pre-disturbance growth rates.

The between-site differences in both the level of impact of the 1998 bleaching event and the subsequent recovery time are not easily explained by between-site differences in heat stress associated with the 1998 bleaching event. I tested the hypothesis that my sites experienced differences in heat stress in 1998 by calculating the degree-heating-weeks (DHW) (Strong et al. 1997) for my four study areas from 7-day composite night time sea surface temperature data (Supplement). My findings indicate that during 1998, heat stress was higher at Cayos Cochinos and the Sapodilla Cayes (6.84 and 5.54 maximum DHW, respectively), compared to Utila and Turneffe Atoll (3.34 and 2.27 maximum DHW, respectively). However, while lower temperature stress may help explain the lower stress banding at Turneffe it cannot explain the lack of resilience at Utila or the higher resilience in Cayos Cochinos (which experienced the highest heat stress).

I also examined the possibility that a hurricane strike may have had different effects across the Mesoamerican Reef. Category 5 hurricane Mitch (October 21-29, 1998) produced extreme runoff over most of the southern portion of the Mesoamerican Reef and reduced water clarity for several weeks (Andréfouët et al. 2002). However, we have found no geochemical signature associated with runoff from Mitch, even in coral cores analyzed at extremely high resolution using laser ablation (Koenig et al. in prep). The lack of signal indicates the corals stopped calcifying due to the bleaching event (August 1998) prior to the hurricane. While poor water quality could explain the subsequent low resiliency of corals at the southern sites, it is notable that corals at the most southerly site, Cayos Cochinos, recover to pre-1998 growth rates just as rapidly as corals at Turneffe where the runoff impact of the hurricane was low. In addition, earlier hurricane strikes have left almost no record in my coral growth rate data; the only year with a major hurricane in which extension rates were significantly suppressed was 1961 in the Sapodilla Cayes, which may have been related to hurricane Hattie. However, Hattie passed directly over Turneffe Atoll and this site has no significant growth effects, suggesting that the overall impact of hurricanes has been low on *Montastraea faveolata*.

I conclude that the large differences in chronic stress between my sites are responsible for differences in coral resilience following exposure to the 1998 bleaching event. To date the 1998 bleaching event remains the most significant bleaching event recorded on the Mesoamerican reef, as the 2005 event was significantly less severe than in other parts of the Caribbean (McField et al. 2005). My data do not support the hypothesis that exposure to stress might help coral colonies acclimatize and therefore resist bleaching. Instead, it is clear that coral colonies experiencing higher local stress before 1998 were *more* severely affected by bleaching (with higher stress banding incidence) and recovered more slowly (in terms of growth rates) than those exposed to lower chronic stress. Possibly, the acclimatization hypothesis is only applicable for the same stressor (i.e. thermal stress) or for lower levels of stress than Sapodilla and Utila experience, and the multi-species coral community may exhibit acclimatization patterns different from the individual coral colony response measured in this study. For example, repetitive bleaching may increase a coral's ability to withstand future heat stress (Brown et al. 2002, Castillo and Helmuth 2005), but other local stressors such as increased sedimentation may depress a coral's energy reserves (Rogers 1990), making it less likely to survive or recover from a bleaching event (Rodrigues and Grottoli 2007). Even if acclimatization can occur in some cases, the differential responses of *M. faveolata* across various stress regimes indicate that local conservation efforts that reduce stress, such as reducing runoff by replanting mangroves at the coast or protecting an area from overfishing, could have significant impacts on the ability of corals to withstand the effects of climate change. Future research could investigate whether this interaction between local and global stressors extends to other coral species.

Table 2-3. Recovery of extension rates after 1998. Results of a generalized linear model estimate for changes in average extension rates after 1998, controlling for trends across years. Extension rates from 1950-1997 and 2002-2006 were compared. Significance levels are not significant (NS) >0.05, *<0.05, **<0.01, ***<0.001.

	High Local Stress Sites		Low Local Stress Sites	
Predictor	**Sapodilla Cayes**	**Utila**	**Turneffe Atoll**	**Cayos Cochinos**
Post 1998	-0.147**	-0.281***	NS	NS
Year	-0.002*	NS	NS	NS
Constant	5.200**	NS	NS	NS
N	53	53	53	53
F	20.70	18.26	2.83	2.19
P	0.000	0.000	NS	NS
R2	0.45	0.42	0.10	0.18

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SUPPLEMENT

Coral Sampling

I collected cores using SCUBA and a hand-held reversible air drill (Ingersoll-Rand 7803RA, 500 rpm) driven by a gasoline-powered air compressor (Westward 4B220, 10 cfm). A custom-built stainless steel core barrel 6 cm in diameter and 50 cm long fitted with a brass drill head containing carbide teeth was fashioned after the design developed by the Australian Institute for Marine Science. After core removal, pre-cast concrete plugs were inserted to prevent colonization inside the coral by boring organisms and allow coral regrowth. At each site, I collected cores from the largest heads within reach of a 100-foot-long hose. Cores were drilled vertically to obtain the clearest banding pattern along the maximum growth axis.

After collection, tissue was removed using a waterpik and the cores were rinsed in fresh water and air-dried. A ~0.86 cm thick slab from the middle of each core was cut using a water-lubricated double-bladed diamond table saw. Finally, core slabs were cleaned in de-ionized water and then air-dried.

X-radiography

Core slabs were x-rayed at the University of California San Diego Thornton Hospital using a Siemens Polyphos 50 with a source-to-object distance of 40 inches and a setting of 63 kilovolts at 5 milliamps/second. Digital x-ray cassettes were processed using an AGFA Musica ADC Compact Plus, and images saved in DICOM format, as well as hard copy films. I measured coral growth rates from x-rays using the program CoralXDS (Helmle et al. 2002).

Anthropogenic Stress

To calculate an index of current anthropogenic stress at my sites, I used the average Ba/Ca from the top 5 years of 5 coral cores from each site to represent sedimentation from Prouty et al. (2008). To represent nutrient input, I calculated the average chlorophyll-a from **t**ime series of satellite-derived monthly chlorophyll-a concentrations from October 1997 to October 2007 at each site obtained from NOAA Coastwatch, using data from the Sea-viewing Wide Field-of-view Sensor (O’Reilly et al. 1998). Chlorophyll-a can be used as a proxy for nutrient input, though the presence of an algal bloom necessarily removes dissolved nutrients from the water column; however the indirect impact beyond that of increased dissolved nutrients is important on coral reefs (Furnas et al. 2005). The relative between-site differences in sedimentation and nutrient input should both be relatively stable over time, as century-scale timeseries of Ba/Ca from each site reveal approximately constant differences between sites (Carilli et al. in review). Human population in Utila and Cayos Cochinos was obtained from 2001 Honduran census data. Human population at Turneffe and Sapodilla was estimated by M. Mcfield based on local knowledge. While all populations have likely increased over the past century, the relative ranking of human population between sites has remained the same. Fishing pressure was estimated from the relative fish population index values from the Healthy Reefs Scorecard (Healthy Reefs Initiative 2008). Fishing pressure is the only measure that may not have retained the same long-term ranking between sites (for instance if fishing expands further offshore as nearby reefs are depleted); however removing this measure does not affect the relative ranking of total impact indices described below. The above four measures of anthropogenic stress: sedimentation, nutrient input, direct human impact, and fishing pressure, were log-transformed (log(X+1)), then rescaled between 0-1 (by subtracting the minimum and dividing by the range) to put them on a unitless scale for direct comparison following Halpern et al. (2008). Each impact value was then multiplied by the coral-reef impact-specific weight determined by Halpern et al. (2007). The weight for artisinal fishing from Halpern et al. (2007) was used for the fishing pressure measure calculated here. All weighted impact values were then summed to calculate the Impact Index, but since the index value used for fishing was calculated using fish abundance (with higher abundance representing less fishing), I subtracted the fish abundance factor. Note that this weighting does not actually affect the impact index rankings; the index calculated using summed unweighted impact values gives the same results. Note also that this approach assumes that impacts will be additive, which may not be correct. However, without additional information on how corals react to the combination of multiple stressors, this is the assumption I make here.

To compare the relative Impact Index rankings for each site with the Halpern et al. (2008) global impact map, I retrieved impact factors from four cells from their map around my sites, and averaged these values. To compare my relative impact rankings to the Healthy Reefs Scorecard Integrated Reef Health Index (IHRI) (Healthy Reefs Initiative 2008), I calculated the average IHRI for reefs that were surveyed close to my sites. For Turneffe, I averaged surveys at 6 sites, for Cayos, 2 sites, for Utila, 3 sites, and for Sapodilla, 3 sites. The IHRI is on a reversed scale compared to the other indices, wherein lower values represent a less healthy reef in the IHRI index. Although these stress and health metrics were calculated for a specific point in time, the measures included probably don't rapidly fluctuate (for instance, shipping traffic and runoff in the Halpern et al. dataset or coral and algae cover in the IHRI dataset).

Calculating Thermal Stress in 1998

Degree heating weeks (DHW) were computed from Advanced-Very-High-Resolution-Radiometer (AVHRR) 7-day composite night-time sea surface temperature data (Li et al. 2001). Between 10-15 grid cells (each 0.5° x 0.5°) were averaged for each site to account for gaps in records from individual grid-cells due to cloud cover. Patterns in SST changes within sites are more highly correlated than those between sites, indicating that using the average of these multiple grid cells to reconstruct DHW over this time period is justified. During several weeks at each site, cloud cover restricted the available data. During these weeks patterns of temperature change at other sites were used to predict temperature at the missing site. For instance, if temperature for a missing week was 0.3 degrees higher than the previous week at sites without cloud cover, I added 0.3 degrees to the previous week's temperature at the site with missing data. While satellite data, or any form of SST data that is not collected at high resolution in situ, will necessarily smooth the temperature signal and not capture the full range of temperatures experienced by the corals (Leichter et al. 2006), these types of data are not available for all sites or over a long time period at any site. However, AVHRR night-time data were quite similar to in situ data collected from Florida Keys reefs (Toscano et al. 2002). Therefore, in this study AVHRR data were used to calculate DHW in 1998 to compare differences in heat stress between sites.

DHW are calculated in several steps. First, hotspots are calculated by subtracting the local mean monthly maximum climatology, calculated by NOAA over the time period 1985-1993 (Strong et al. 1997), which was 28.9°C for all of the sites. Hotspots are defined as any measurement that exceeds this mean temperature (Strong et al. 1997). DHW are then calculated in moving windows, by summing the previous 12 weeks of hotspots that are at least 1°C above the mean climatology (Strong et al.

1997). Here, I calculated the maximum DHW during 1998 at all sites and also summed all of the DHW for 1998 to compute the cumulative DHW for each site. Both of these measures result in the same heat stress ranking between sites: Cayos Cochinos with the highest heat stress, followed by the Sapodilla Cayes, Utila, and Turneffe Atoll.

Carbonate Saturation

Unfortunately, no long-term datasets of carbonate saturation are available for the Mesoamerican Reef. A study in summer 1961 and 1962 found that all waters across the Belizean portion of the Mesoamerica Reef were supersaturated with respect to carbonate, but that those in southern Belize were less so than in the north (Purdy et al. 1975). This pattern is probably related to the higher influence of freshwater in the south. This overall pattern cannot explain why corals at Cayos Cochinos (also presumably experiencing similar levels of carbonate saturation as Sapodilla) recovered, while those at Sapodilla did not.

Coral Cover Before and After 1998

Percent coral cover pre-and post-1998 from Sapodilla, Turneffe, and Utila were compiled (McField 2000, Afzal et al. 2001, McField et al 2005) and benthic point intercept transect surveys completed by myself and Sheila Walsh in October, 2005 using the Mesoamerican Barrier Reef System Synoptic Monitoring Program methods (Almada-Villela et al. 2003) (Fig. 2-S1).

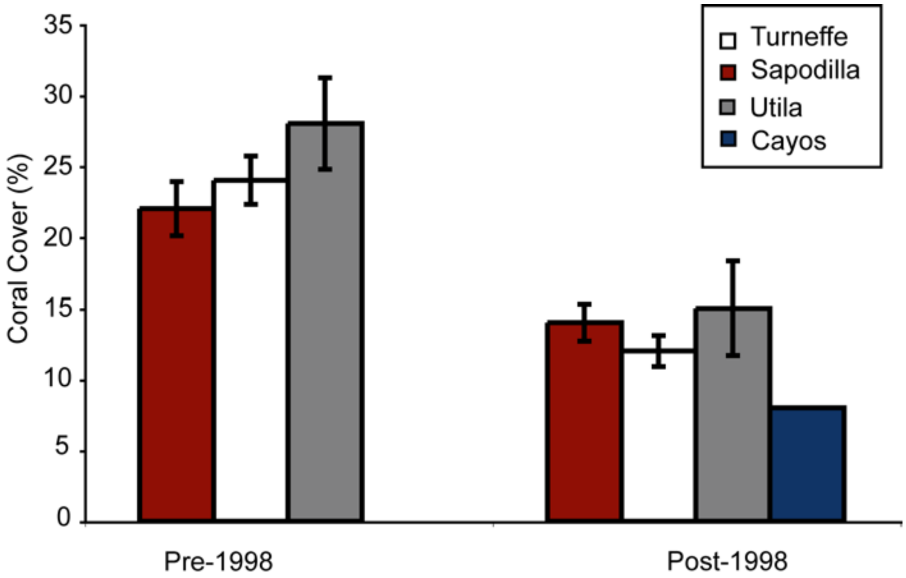

Figure 2-S1. Coral cover pre- and post-1998. Pre-1998 data from Turneffe and Sapodilla from McField (2000) and from Utila from Afzal et al. (2001). No pre-1998 data are available from Cayos Cochinos. Post-1998 data from Turneffe and Sapodilla from surveys by Sheila Walsh and myself, October 2005. Post-1998 data from Utila from Afzal et al. (2001) and from Cayos from McField et al. (2005). Error bars represent standard error.

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CHAPTER 3: Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold

ABSTRACT

Coral bleaching, during which corals lose their symbiotic dinoflagellates, appears to be increasing in frequency and geographic extent, and is typically associated with abnormally high water temperatures and solar irradiance. A key question in coral reef ecology is whether local stressors reduce the coral thermal tolerance threshold, leading to increased bleaching incidence. Using tree-ring techniques, I produced master chronologies of growth rates in the dominant reef builder, massive *Montastraea faveolata* corals, over the past 75-150 years from the Mesoamerican Reef. These records indicate that the 1998 mass bleaching event was unprecedented in the past century, despite evidence that water temperatures and solar irradiance in the region were as high or higher mid-century than in more recent decades. We tested the influence on coral extension rate from the interactive effects of human populations and thermal stress, calculated here with degree-heating-months (DHM). Ifind that when the effects of chronic local stressors, represented by human population, are taken into account, recent reductions in extension rate are better explained than when DHM is used as the sole predictor. Therefore, the occurrence of mass bleaching on the Mesoamerican reef in 1998 appears to stem from reduced thermal tolerance due to the synergistic impacts of chronic local stressors.

INTRODUCTION

Coral reefs are threatened by many human induced-impacts, including overgrowth by fleshy macroalgae, whether due to algal growth stimulation from nutrient pollution and/or a reduction in herbivory due to overfishing (Hughes 1994, Lapointe 1997, McCook 1999, McCook et al. 2001, McClanahan et al. 2003, *Smith et al.* 2006); abrupt smothering or a slow reduction in fitness due to sedimentation (Dodge and Vaisnys 1977, Rogers 1990, Reigl and Branch 1995, Fabricius and Wolanski 2000); and direct damage due to destructive fishing practices (McManus et al. 1997), irresponsible tourism (Barker and Roberts 2004), and boat damage (Saphier and Hoffmann 2005). Coral diseases and bleaching (the phenomenon in which corals lose pigmentation associated with their symbiotic dinoflagellates, typically due to thermal stress) both appear to have increased in recent decades (Harvell et al. 1999, Hoegh-Guldberg 1999) while live coral cover has declined (Gardner et al. 2003). Although reef degradation can be gradual, abrupt and severe episodes such as mass bleaching events can also lead to the sudden loss of corals (McField 1999). An outstanding question is whether the amount of thermal stress a coral can tolerate before bleaching (Fitt et al. 2001) is affected by other local stressors (Knowlton & Jackson 2008, Sandin et al. 2008). Conversely, some authors argue that recent declines in coral reef health are due to novel stressors that have increased in recent decades, such as an increase in pathogens (Shinn et al. 2000, Aronson et al. 2003), and not threshold effects associated with multiple interacting stressors. However, a recent study investigating coral bleaching on the Great Barrier Reef found that thermal tolerance indeed decreased with increased dissolved inorganic nitrogen sourced from land (Wooldridge 2009), suggesting that recent coral demise is not necessarily related to novel stressors but the interaction of unprecedented levels of multiple stressors. Here I consider the effect of increasing general human impacts on the thermal tolerance threshold in *Montastraea faveolata*, using nearby human population over the past century as a proxy.

Scleractinian corals contain annual growth bands in their skeleton, which are revealed by x-rays (Knutson et al. 1972), and these preserved records of growth can be used to investigate how environmental change has affected coral health. Several studies have found that bleaching reduces skeletal growth in corals, leaving a record in the skeleton, often recognized by a high-density "stress band" (Leder et al. 1991, Mendes and Woodley 2002, Hendy et al. 2003a, Suzuki et al. 2003, Rodrigues and Grottoli 2006). Coral bleaching appears to be increasing in frequency worldwide (Hoegh-Guldberg 1999, Hughes et al. 2003). Despite a record of ecological surveys dating back to the 1950s in Jamaica the first large-scale coral bleaching events were not observed until the 1980's (Goreau 1992). Likewise, in coral skeletal records from Florida, Halley and Hudson (2007) found no record of bleaching before the mid-1980s, after which time multiple bleaching events were identified. On the Mesoamerican Reef, the first mass bleaching event wasn't recorded by observers using SCUBA until 1995 (McField 1999) followed by a more severe event in 1998 (McField 2000, Aronson et al. 2002a).

I investigated the history of bleaching on the Mesoamerican reef by applying tree-ring techniques to construct annually resolved, multidecadal records of growth from skeletal cores of massive *Montastraea faveolata* corals. Growth chronologies and bleaching incidence were then compared with records of thermal stress and solar irradiance, as well as human impacts, using the population of Honduras as a proxy (population in 2006 ~7.4 million). The population of Honduras is a good indicator of local human impacts because over 80% of land-based runoff in the region originates from Honduras, and this has increased over time along with population (Burke and Sugg 2006). Indeed, Burke and Sugg (2006) modeled sediment and nutrient runoff in watersheds surrounding the Mesoamerican Reef for the current land use scenario and that for the hypothetical natural cover. They found that sedimentation increased over 20-fold, discharge doubled, nitrogen increased 3-fold and phosphorus increased 7-fold. Meanwhile, the human population has more than tripled in Honduras and Guatemala since the 1950's (United Nations 2008). I investigated whether the history of coral bleaching on the Mesoamerican Reef could be explained by thermal stress alone, or whether bleaching was better explained by the combination of recent local human impacts and thermal stress.

MATERIALS AND METHODS

Coral Collection and Preparation

Ninety-two coral cores from *Montastraea faveolata*, the dominant reef-builder on the fore-reef (Mcfield 2000) were collected at four sites on the Mesoamerican reef:

Turneffe Atoll, and the Sapodilla Cayes in Belize; and Utila and Cayos Cochinos in Honduras (Fig. 3-1, Table 3-1). Cores were collected between 2.5-13 m depth in spur and groove habitat using a hand-held reversible air drill driven by a gas-powered air compressor. A custom-built stainless steel core barrel 6 cm in diameter and 50 cm long fitted with a brass drill head containing carbide teeth was fashioned after the design developed by the Australian Institute for Marine Science. After core removal, pre-cast concrete plugs were inserted to prevent colonization of the inside of the coral by boring organisms and allow coral regrowth. At each site, I collected cores from the largest heads within a 30-meter radius from the anchor/buoy site. Cores were drilled vertically to obtain the clearest banding pattern along the maximum growth axis. Several cores were collected from dead coral heads to avoid biasing the record by analyzing growth rates only from survivors. After collection, tissue was removed using a waterpik and the cores were rinsed in fresh water and air-dried. A slab of 0.86 cm thickness was cut from the middle of each core using a water-lubricated double-bladed diamond table saw. Finally, core slabs were cleaned in de-ionized water and air-dried.

Core slabs were x-rayed at UCSD Thornton Hospital using a Siemens Polyphos 50 with a source-to-object distance of 40 inches and a setting of 63 kilovolts at 5 milliamps/second. Along with each core, 4 cm wide aluminum bars of the same thickness as the coral slabs (0.86 cm) were irradiated (Fig. 3-2). An aragonite wedge cut from a *Tridacna maxima* clam shell and three aluminum wedges, including one of the same dimensions as the shell were also irradiated to calibrate skeletal density based on x-ray brightness (Fig. 3-2). Digital x-ray cassettes were processed using an AGFA Musica ADC Compact Plus, and images saved in DICOM format, as well as hard copy films.

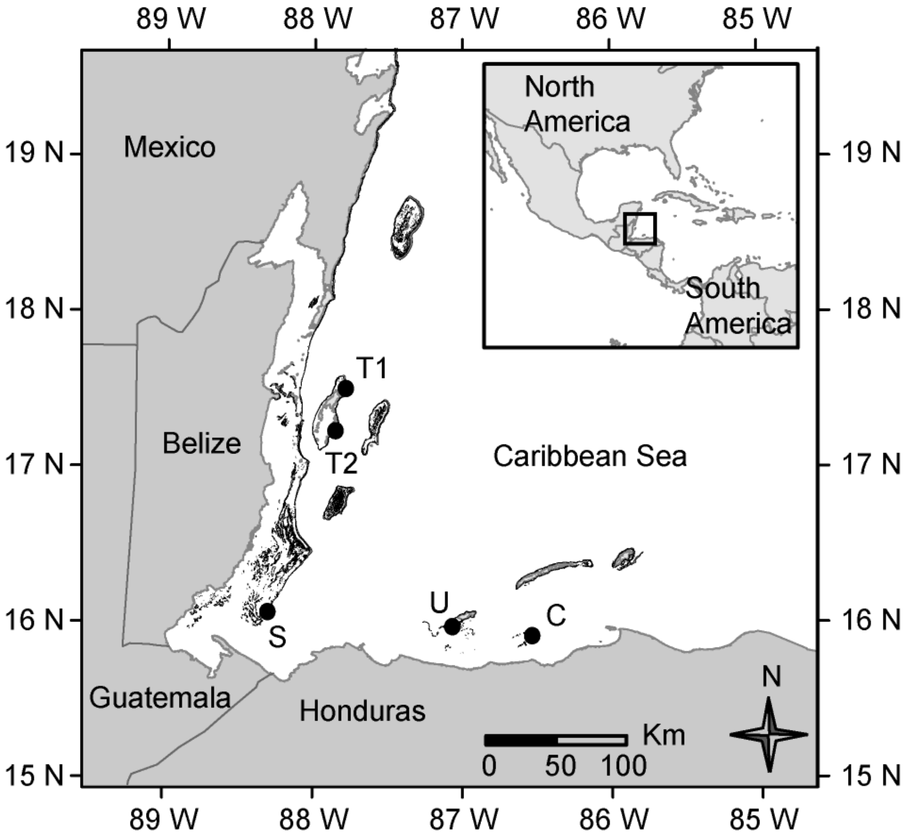


Figure 3-1. Map of the Mesoamerican Reef showing locations of coral collections as black circles. Dark gray denotes coral, light gray denotes land areas. T1, T2 = Turneffe Atoll (4 cores from T1, 13 from T2), S = Sapodilla Cayes, U = Utila, C = Cayos Cochinos.

Table 3-1. Coral core collection site locations, with dive site name or nearby caye, coordinates, number of cores from each site, along with growth anomalies in 1998 and earlier. Table lists the total number of cores which were drilled and slabbed along the growth axis, the percentage and number of these that have dense stress bands associated with the 1998 event, the percentage and number that contained a partial mortality scar, and any previous individual stress bands.

Site	Dive Site Name	Coordinates	Total Cores	1998 Stress Band	Partial Mortality in 1998	Previous Stress Bands
Turneffe 1	Dog Flea Caye	17°29’59”N, 87°45’30”W	17	71% (12)	6% (1)	2
Turneffe 2	Harry Jones	17°18’25”N, 87°48’04”W				
Sapodilla	Frank’s Caye, NE buoy	16°07’45”N, 88°14’59”W	44	100% (44)	16% (7)	0
Utila	Diamond Caye	16°03’52”N, 86°57’30”W	17	100% (17)	12% (2)	1
Cayos Cochinos	Pelican Point, Peli 2	15°58’41”N, 86°29’06”W	14	100% (14)	21% (3)	0
		Total	**92**	**95% (87)**	**14% (13)**	**3**

DICOM images were converted to BMP format using ImageJ (Rasband 2007). I analyzed coral x-rays for annual linear extension, density, and calcification (the product of extension and density) using CoralXDS and the second derivative zero band delimiting function therein to objectively identify the beginning and end of each band (Helmle et al. 2002). The "heel effect," caused by differing intensity of the x-ray field along the anode-cathode axis (Carlton and McKenna-Adler 1912), could influence density measurements and estimates of calcification. Using the same principle as a Carricart-Ganivet and Barnes (2007), the aluminium slabs irradiated in each coral x-ray were used to construct a background image with the same dimensions as the full x-radiograph. Each background image was then subtracted in CoralXDS to remove the heel effect. Note for the 2 longest cores from Utila, the heel effect could not be sufficiently removed, so only extension rates are shown. For each coral core, 3 transects at various locations on the core were analyzed and averaged to account for slight variations in within-band extension and density. Transects were measured alongside of the axis of maximum growth. The vertical coral growth axis was avoided because growth band curvature within the maximum growth axis can artificially affect the measured parameters.

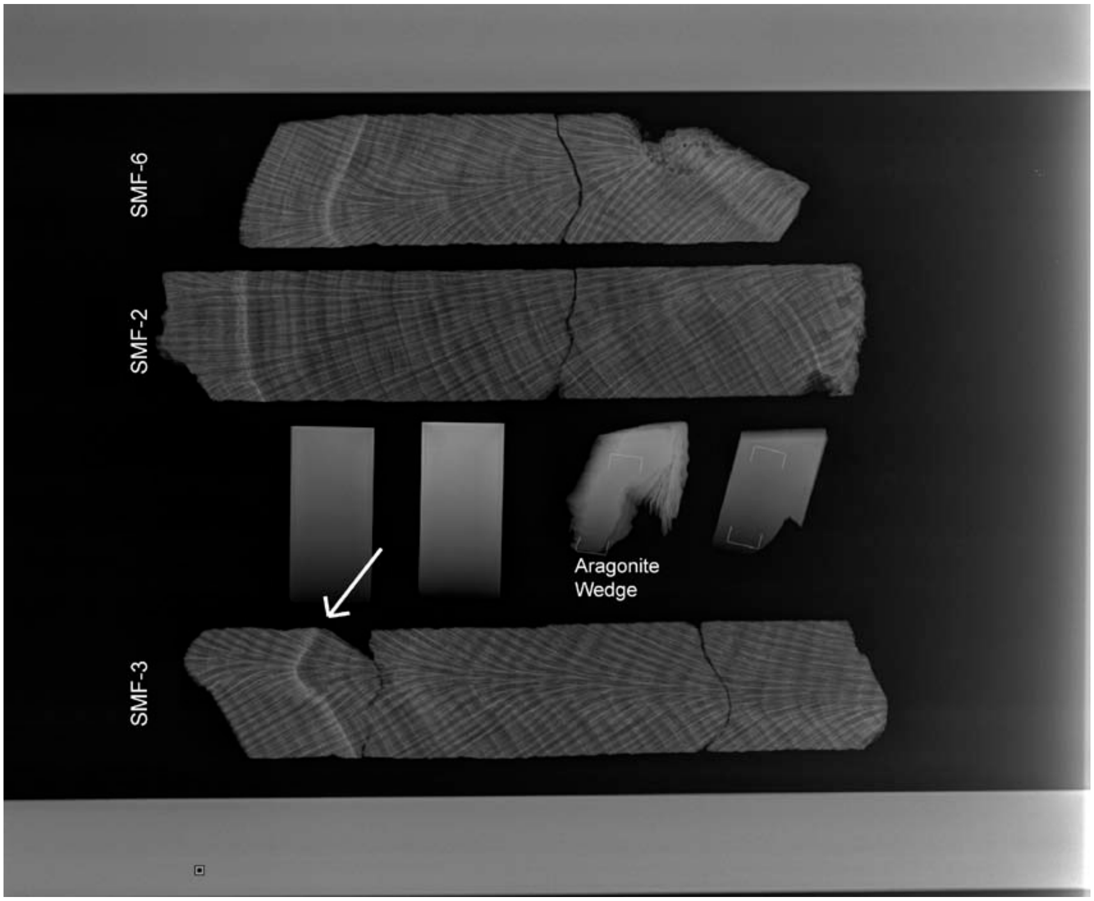


Figure 3-2. X-radiograph of 3 short cores from the Sapodilla Cayes. Core name labels and core tops are at left. Aluminum bars are on the top and bottom of the x-ray. Note the compressed growth in 1998 revealed as a bright, dense band and denoted by an arrow on the bottom core. Aragonite wedge is labeled, other wedges are aluminum.

Chronology Development

In the first step of chronology development, I ensured that all growth increments were assigned the correct calendar year through the tree-ring technique of crossdating (Fritts 1976). Crossdating relies on the principle that individuals from a given site share growth patterns if the same limiting environmental factors control growth. The technique consists of matching synchronous growth patterns among multiple samples, beginning at the most recently formed increment and working back in time. If an increment is accidentally missed, the growth pattern in that individual will be offset by a year relative to the others in the sample set, indicating an error. In so doing, crossdating ensures the annual resolution of the final chronologies. Some corals contain distinct patterns in luminescent banding which can assist with chronology development (*Montastraea* corals from Florida, Hudson et al. 1994; *Porites* corals from Australia, Hendy et al. 2003b). However, no distinctive luminescent banding was evident in the *M. faveolata* from Mesoamerica. Instead, crossdating these corals relied on patterns in growth-increment width.

I used the program COFECHA to statistically validate crossdating (Grissino-Mayer 2001). This program detrends each measurement time series with a cubic spline set to a 50% frequency response of 32 years and then removes any remaining autocorrelation so that the final time series meet the assumption of serial independence and have a mean of one. Next, COFECHA correlates each standardized time series with the average of all other standardized time series. A low correlation indicates a potential error and that the sample should be visually re-inspected for false or missing bands. COFECHA was also used to verify the dating of cores collected from dead corals, based upon correlation with the live-collected cores. COFECHA also calculates series intercorrelation, the mean correlation between each standardized time series and the average of all others in the sample set. The high-frequency, between-year growth variability is described using the mean sensitivity, which for any pair of adjacent years ranges from zero (each year is the same width) to two (when a non-zero value is adjacent to a zero value; i.e. a missing increment) (Fritts 1976) (Table 3-2). All samples with non-significant series intercorrelation values were visually checked and no errors were found. In addition, no series intercorrelation values were extremely low (lowest r = 0.18).

Extension rates had higher series intercorrelations compared with density and calcification (Table 3-3), and were therefore used for statistical trend analyses. Although calcification rate accounts for both skeletal extension and density, here Ifind that density does not vary widely and is not well correlated between heads, as exemplified by the lower series intercorrelation values. Instead, calcification in these corals appears to be mostly driven by fluctuations in extension (average R^2 between extension and calcification master chronologies = 0.76, and between density and calcification = -0.24), as identified earlier by Lough and Barnes (2000). In addition, during and after the 1998 bleaching event, I find suppressed extension rates and increased density, especially at Sapodilla and Utila, though calcification remains almost constant. This indicates that analyses of calcification rates would ignore a potentially important biological signal, perhaps due to trade-offs between extension and density that do not affect overall calcification (Carricart-Ganivet and Merino 2001, Carricart-Ganivet 2004).

A total of 46 cross-dated cores were used to construct long-term master chronologies of coral growth; this subset had been accurately drilled and cut along the axis of maximum growth and therefore had clear x-rays (Table 3-1). First, each coral measurement time series was standardized by dividing by the mean growth-increment width. Standardized time series, each with a mean of one, were then averaged to produce the master chronology at each site (Fritts 1976). Extension rate master chronologies are plotted in Fig. 3-3, while all three measures are plotted in Fig. 3-4. Because corals are not known to have any size or age-related growth trends, the records were not detrended with negative exponential functions or cubic splines as with tree-ring records (Fritts 1976). Note that I do not evaluate differences in absolute growth rate, which do not necessarily reflect reef health (Edinger et al. 2000). Instead, Iinvestigated long-term trends in relative growth rates to more accurately evaluate the impacts of coral bleaching within and among sites. Differences in both absolute extension rates among and within sites are discussed in Carilli et al. (in press).

Table 3-2. Series intercorrelation and average mean sensitivity of extension rates from corals at each site as calculated using COFECHA. The number of total correlated segments and the number of flagged segments (segments with p > 0.01) are also reported.

Site	Series Intercorrelation	Average Mean Sensitivity	Flagged, Total Segments
Turneffe Atoll	.484	.190	0, 15
Utila	.575	.177	3, 19
Cayos Cochinos	.531	.175	3, 22
Sapodilla Cayes	.611	.195	5, 42

Table 3-3. Interseries correlation values for the three growth measurements for each site.

Site	Extension	Density	Calcification
Turneffe Atoll	.646	.214	.625
Utila	.575	.285	.686
Cayos Cochinos	.531	.165	.374
Sapodilla Cayes	.611	.280	.511

Figure 3-3 (facing page). Master chronologies of extension rates for each site (top) and the number of cores in each chronology (bottom). See Fig. 3-4 for density and calcification records. Confidence intervals are the standard error for each year. Major hurricanes that passed close to each site are shown as arrows and are named, and the bleaching events of 1995 and 1998 are shown as vertical orange lines. Note that Sapodilla and Utila both show slight decreases in extension rates before 1998 (GLM: Sapodilla, $F_{(2,45)}=7.41$, $P<0.01$, $R^2=0.25$; Utila, $F_{(4,43)}=3.66$, $P<0.05$, $R^2=0.25$).

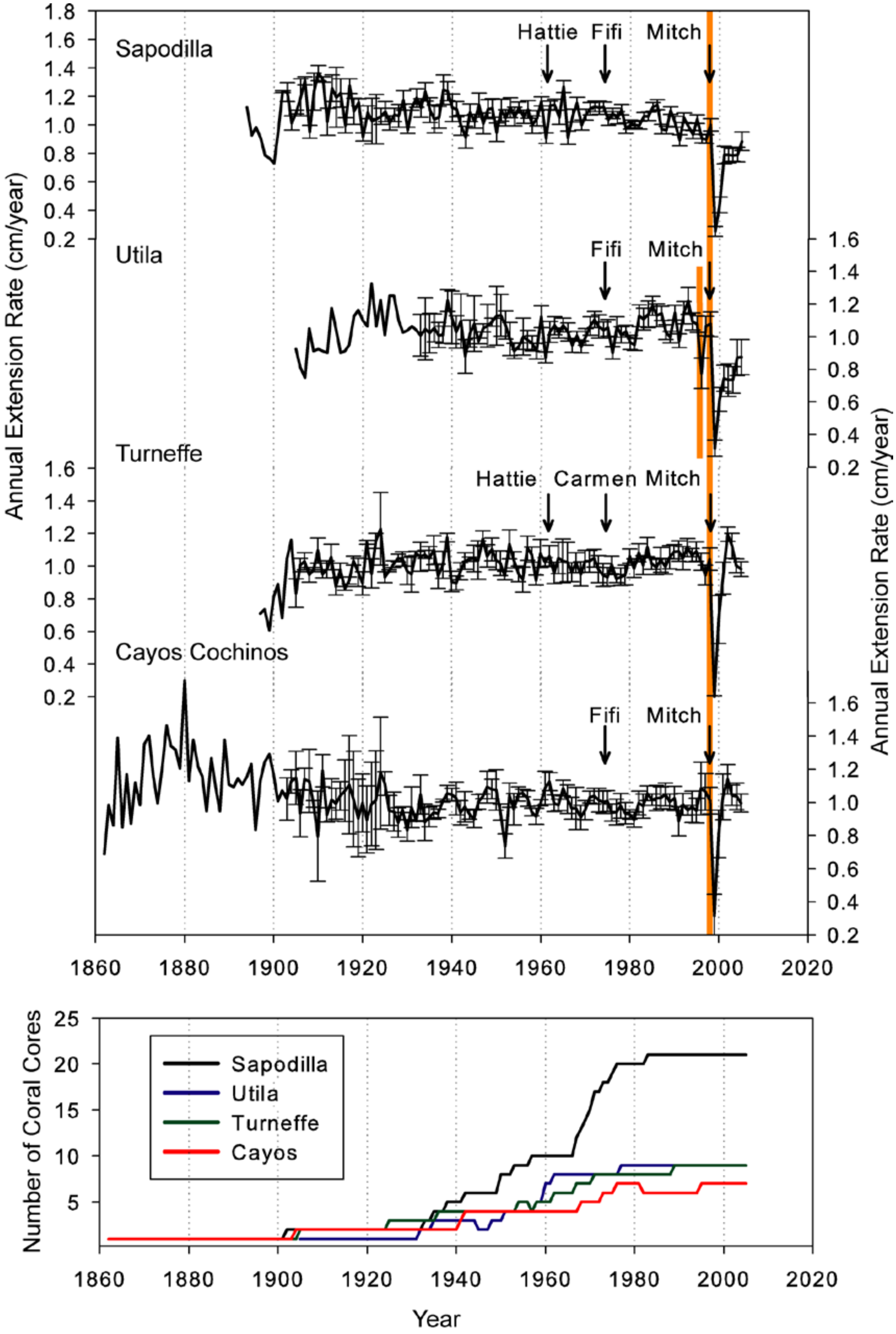
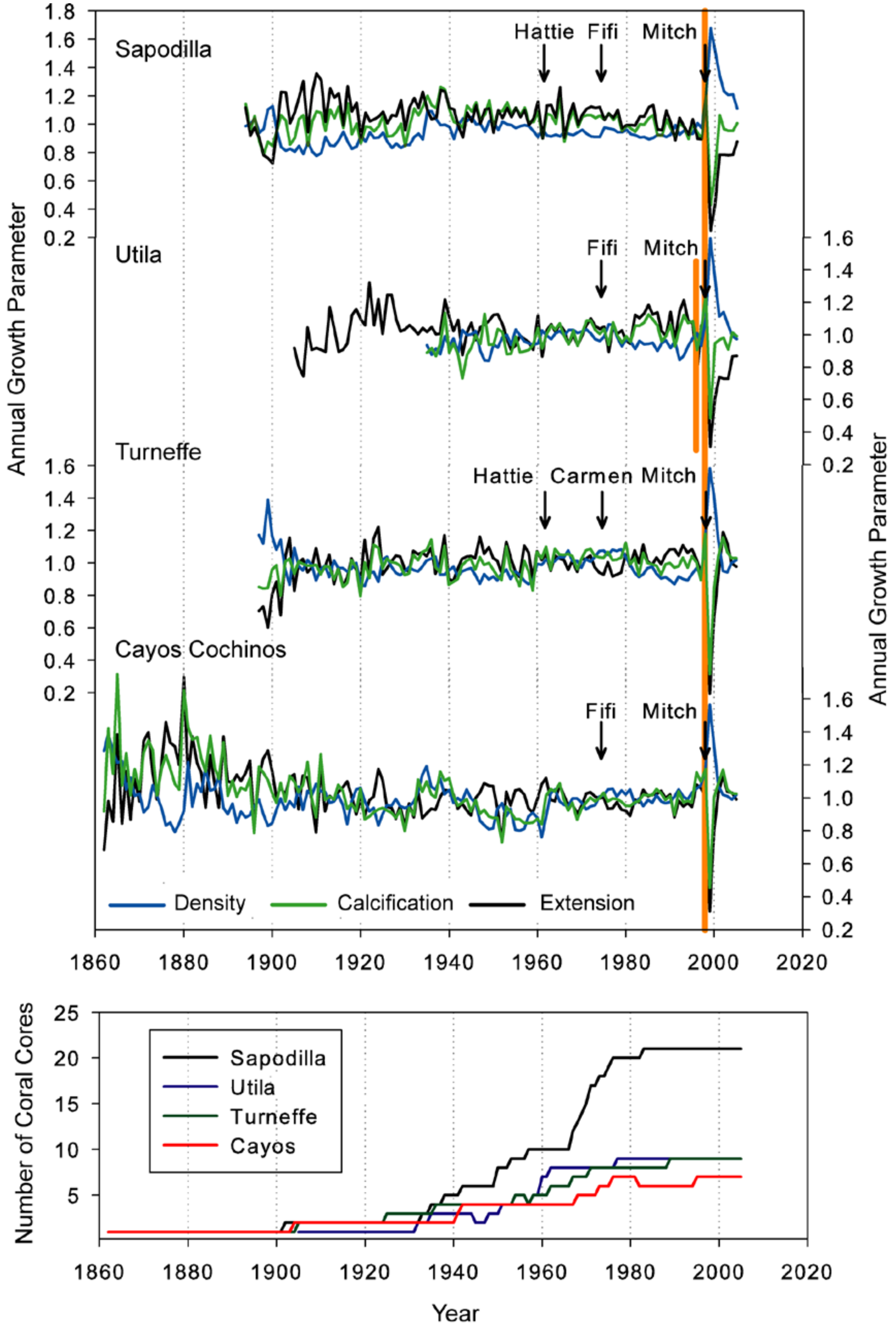

Sapodilla
Hattie
Fifi
Mitch
Utila
Fifi
Mitch
Turneffe
Hattie
Carmen
Mitch
Cayos Cochinos
Fifi
Mitch
Annual Extension Rate (cm/year)
Annual Extension Rate (cm/year)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
1860
1880
1900
1920
1940
1960
1980
2000
2020
Number of Coral Cores
25
20
15
10
5
Sapodilla
Utila
Turneffe
Cayos
Year

Figure 3-4 (facing page). Master chronologies of extension (cm), density (g/cm^3) and calcification (g/cm^2) for each site (top) and the number of cores in each chronology (bottom). Major hurricanes that passed close to each site are shown as arrows and are named, and the bleaching events of 1995 and 1998 are shown as vertical orange lines.

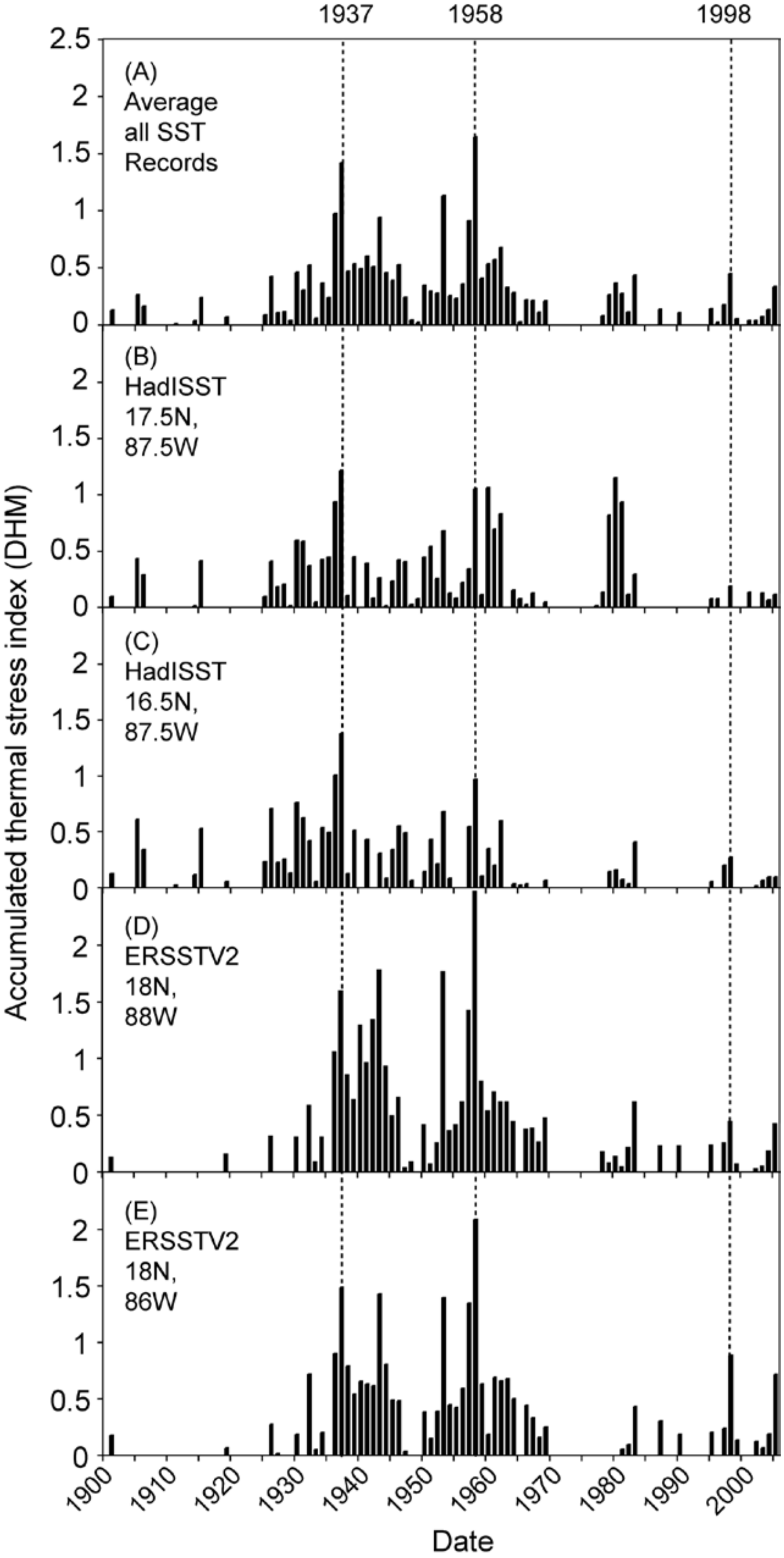

Annual Growth Parameter
Sapodilla
Hattie
Fifi
Mitch
Utila
Fifi
Mitch
Turneffe
Hattie
Carmen
Mitch
Cayos Cochinos
Fifi
Mitch
Density
Calcification
Extension
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
1860
1880
1900
1920
1940
1960
1980
2000
2020
Number of Coral Cores
25
20
15
10
5
Sapodilla
Utila
Turneffe
Cayos
Year

Calculating Thermal Stress

Century-scale records of sea surface temperature (SST) are available on a monthly averaged basis. Given this temporal resolution, I calculated long-term records of thermal stress in terms of degree-heating-months (DHM) (Lough 2000) using a methodology similar to that for degree-heating-weeks, which is a common way of quantifying coral thermal stress (Strong et al. 1997) (Fig. 3-5). Briefly, this method calculates DHM as the annual sum of the difference between average monthly SSTs that exceeded the long-term maximum monthly mean. I obtained long-term records of SST from two different globally-gridded datasets; HadISST and ERSSTV2. Because of the grid sizes in each dataset, individual grid boxes for each site were not available; instead I chose 2 grid boxes from each dataset to represent the region. From the HadISST dataset (Rayner et al. 2003), I chose the 1x°1boxes centered on 17.5ºN, 87.5ºW to represent Turneffe and 16.5ºN, 87.5ºW to represent the southern sites. From the ERSSTV2 dataset (Smith and Reynolds 2004), I chose the 2x2° boxes centered on 18ºN, 88ºW to represent Turneffe and Sapodilla and 18ºN, 86ºW to represent Cayos Cochinos and Utila. Heat stress in Jamaica (Fig. 3-6) was quantified using the ERSSTV2 dataset box centered on 18ºN, 78ºW representing Discovery Bay.

Total annual thermal stress was calculated for each “coral-year”, starting in October of one year and ending September of the next year (Fig. 3-5). To determine whether the long-term SST datasets accurately represented the temperatures experienced by the corals in Mesoamerica, I obtained 2 years (April 2000-May 2002) of in situ temperature measurements (0.0001 degree resolution) taken every ten minutes at Cayos Cochinos (at 5 m depth and the same site as my samples were collected) from the United States Geological Survey. In addition, I compared the in situ and long-term datasets to shorter, higher resolution time series from satellite measurements (Fig. 3-7): AVHRR from Glover’s Reef, Belize (NOAA Coral Reef Watch) and the Integrated Global Ocean Services System (IGOSS) centered on 15.5ºN, 86.5ºW (Reynolds et al. 2002). While the long-term records, due to their coarser temporal resolution, do not capture the full range of short-term variability, the DHM measure has been shown to accurately predict bleaching in the western Indian Ocean (McClanahan et al. 2007). I also obtained data from the Comprehensive Ocean-Atmosphere Data Set on the density of shiptracks that supply most of the early SST data to verify that data are reliable (Woodruff et al. 1987). Those data after 1950 are based on a greater number of observations and are therefore more reliable.

Figure 3-5 (facing page). Accumulated annual temperature stress. Temperature stress was calculated by summing the monthly temperature anomalies that exceed the long term average of the maximum monthly temperatures. Records from 2 grid cells (denoted by the latitude and longitude of the center of each cell) from each of 2 long-term temperature records: HadISST (Rayner *et al.* 2003) and ERSSTV2 (Smith and Reynolds 2004) are used, and the average of these four records is also shown (A). (B) and (D) represent Turneffe, (C) and (D) represent Sapodilla, and (C) and (E) represent Cayos Cochinos and Utila. Years with the highest heat stress in the average of all four temperature records are denoted by a dashed line.


1937
1958
1998
(A)
Average
all SST
Records
(B)
HadISST
17.5N,
87.5W
(C)
HadISST
16.5N,
87.5W
(D)
ERSSTV2
18N,
88W
(E)
ERSSTV2
18N,
86W
Accumulated thermal stress index (DHM)
2.5
2
1.5
1
0.5
0
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
2000
Date

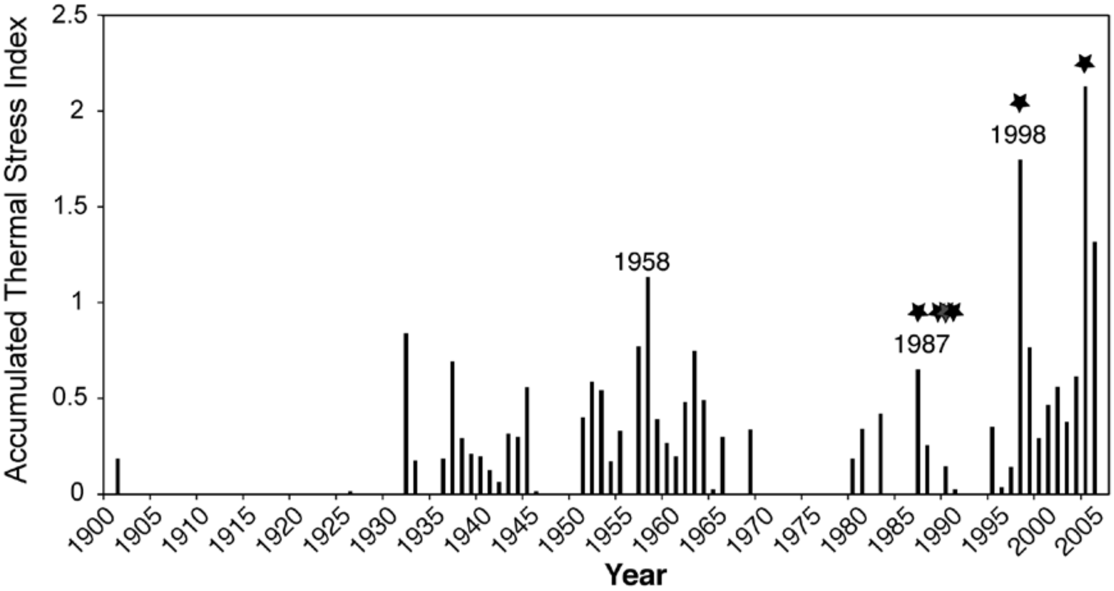


Figure 3-6. Accumulated thermal stress for Discovery Bay, Jamaica. Temperature stress was calculated by summing the monthly temperature anomalies that exceed the long term average of the maximum monthly temperatures. Data from the ERSSTV2 dataset (Smith and Reynolds 2004), centered on 18°N, 78°W was used. Stars indicate recorded mass bleaching in 1987, 1989, 1990, 1991, 1998, and 2005.

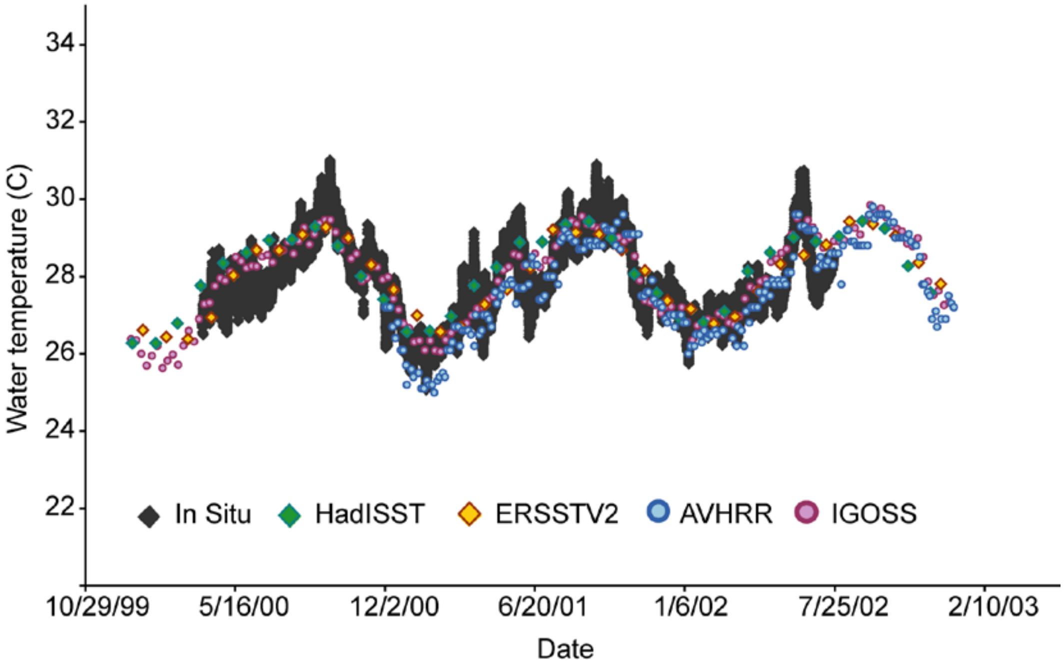


Figure 3-7. Cayos Cochinos water temperature data from several sources. Water temperature data from in situ measurements at Pelican Point, Cayos Cochinos (measurements every 10 minutes, black) is compared with monthly long-term data from the HadISST (green) (Rayner et al. 2003) and ERSSTV2 (yellow) (Smith and Reynolds 2004) datasets, along with more recent satellite measurements from AVHRR (blue) (NOAA Coral Reef Watch) and IGOSS (pink) (Reynolds et al. 2002) datasets.

Solar Irradiance

In order to compare levels of solar irradiance in 1998 to those during warm periods in the middle of the twentieth century (Fig. 3-5), Iplotted the average monthly cloudiness for a grid cell centered on 17ºN, 87ºW from COADS (Woodruff et al. 1987) (Fig. 3-8). Cloudiness is expressed in oktas: the number of eighths of the sky covered by clouds on a scale from 0 (no clouds) to 8 (completely covered).

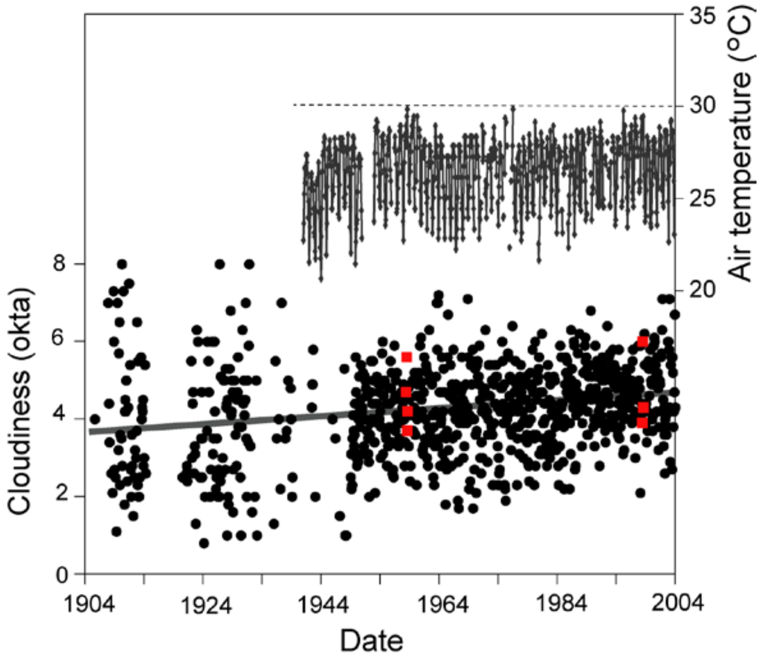


Figure 3-8. (Top) Air temperature record from the Goldson International Airport, 1941-2004. Warm air temperatures in the late 1950's support my confidence in long sea surface temperature records. Dashed line delineates 30ºC air temperature. (Bottom) Monthly cloudiness record (black circles) from the grid cell centered on 17ºN, 87ºW, expressed in oktas, the number of eighths of the sky covered by clouds. A linear trend line is plotted in gray and the months June-September in 1958 and 1998 are shown for comparison (red boxes).

Data Analysis

The number of cores that comprise each master chronology decreases with age (Fig. 3-3), and the variance increases accordingly. Master chronologies must be interpreted with caution prior to approximately 1950 where the number of contributing colonies becomes quite low, often less than five. As noted above, in comparison with density and calcification, coral extension rates had the strongest common signal as gauged by the tree-ring statistic of series intercorrelation (Table 3-2), and were therefore the only measure of coral growth retained for further analysis.

I tested for trends using the master chronology growth rates from 1950-2007 to avoid bias associated with the decrease in chronology power with age. The timing of changes in extension rates from 1950 to 1997 was estimated by fitting a generalized linear model ($extension = \beta_0 year + \beta_1 year * post1955 + ... + \beta_9 year * post1995$) (Table 3-3). Categorical variables representing time periods starting every five years after 1950 were included in the model. The categorical variable, post19XX, were assigned a value of one for years 19XX to 1997 and zero otherwise. Variables were eliminated using a stepwise backward regression method with a tolerance of p=0.2.

I used stress bands to investigate the history of coral bleaching. Stress bands were assumed to represent bleaching events and were identified as bands in which density exceeded the series average by at least 1.5 standard deviations. However, a potential complication to this reconstruction is that the surface of a coral head may not completely bleach (Rowan et al. 1997). Thus, a single core may not record a bleaching event if it passes through a region of the coral head that was not fully impacted. To address this issue, Hendy et al. (2003a) calculated the likelihood of sampling previous bleaching events based on the number of cores collected and the proportion of coral surface area that was bleached. I also calculated the likelihood that a prior mass bleaching event occurred, but was not recorded in my cores, using the incidence of stress banding in my cores and the equation: $probability = \left[\frac{n!}{r!(n-r)!}\right] p^r (1-p)^{n-r}$, modified from Hendy et al. (2003a), where n is the number of cores collected, r is the number of the collected cores with a stress band, and p is an estimate of the proportion of each colony that bleached. Although the scale of the 1998 bleaching event was extensive, and therefore the proportion of a colony's surface that was bleached may have been higher, I used p=0.3 as a conservative proportion as in Hendy et al. (2003a).

To test for interactive effects on coral extension rate between DHM and human impacts, I fit a generalized linear model using extension rates, DHM of the previous year and the population of Honduras (United Nations 2008) as a proxy for human impacts. I used DHM for the previous year because reduced coral growth due to bleaching typically occurs at the tail end of each "coral-year," and therefore the following year records a smaller amount of skeletal accretion. I fit the model $(extension_t = \beta_0 + \beta_1 * DHM_{t-1} + \beta_{2*} popXXpercentile_t + \beta_3 * DHM_{t-1} * popXXpercentile_t)$ where popXXpercentile was a categorical variable representing whether the population in a given year was greater than or less than the 75th, 80th, 85th, 90th, and 95th percentile of population, taking value one if it was greater than or equal to the value of the specified percentile and zero if it was less. The DHM used here was the average from both grid-cells and datasets (Fig. 3-5A), and I pooled extension rates from all four sites. The best model for each percentile was chosen by stepwise backward regression with tolerance p=0.2. Model fits between percentiles were then compared using the Akaike Information Criterion, and the 90th percentile (~5.8 million people) had the best fit.

RESULTS

At Turneffe and Cayos Cochinos, there are small but significant increases in extension rate during several time periods after 1950 (Table 3-3). Sapodilla Cayes has a slight decline in extension rates starting after 1975 ($p<0.2$) and a significant, steeper decline after 1990 (GLM: $F_{(2,45)}=7.41$, $p<0.01$, $R^2=0.25$, Table 3-3) while Utila has a significant decline after 1995 (GLM: $F_{(4,43)}=3.66$, $p<0.05$, $R^2=0.25$, Table 3-3).

I collected a total of 92 coral cores of which 87 (95%) have a stress band associated with the 1998 bleaching event (Table 3-1). There are only 3 individual years in different cores that contain a high-density stress band (defined here as density over 1.5 standard deviations higher than the mean) before 1998. One of the prior stress bands occurs in a core from Utila during 1995. The likelihood of missing an event on the scale of the 1998 bleaching event in my cores is vanishingly small ($p<<0.0001$) because of the large sample size. Therefore, the 1998 bleaching event was unprecedented by a prior mass bleaching event since at least 1900.

My long-term DHM records show that on the Mesoamerican reef, heat stress was even higher in earlier years such as 1937 and 1958 than 1998 (Fig. 3-5), which agrees with the findings of Lough (2000) for the entire Caribbean region. Mid-century warmth is also supported by air temperature data from the Goldson International Airport (near Belize City). The cloudiness data demonstrate that solar irradiance was not exceptionally high in 1998 (Fig. 3-8). In Jamaica, the first bleaching events occurred in the 1980s (Goreau 1992), but heat stress during those years was lower than during mid-century as well (Fig. 3-6).

The results of the generalized linear model showed that the best model was one where extension rates were affected by DHM_{t-1} as well as the interactive effect of high population and DHM_{t-1}, which changed the slope of the relationship ($F_{(3,409)}= 26.92$, $p< 0.0001$, $R^2=0.32$) (Fig. 3-9).

Table 3-3. Long-term trends in extension rates. Results of GLM estimate for trends in extension over 1950 to 1997. A dash indicates that the variable was excluded from the model using stepwise backward regression with a tolerance of p<0.2. Significance levels are *<0.05, **<0.01, ***<0.001.

	High Local Stress		Low Local Stress	
Predictor	**Sapodilla Cayes**	**Utila**	**Turneffe Atoll**	**Cayos Cochinos**
Year	--	--	-0.005**	-0.009**
Post 1955*Year	--	<-0.0005	--	<0.0005
Post 1960*Year	--	<0.0005	0.066	<0.0005*
Post 1965*Year	--	--	--	--
Post 1970*Year	--	--	--	<0.0005
Post 1975*Year	<-0.0005	--	--	--
Post 1980*Year	--	--	0.120**	<0.0005
Post 1985*Year	--	<0.0005*	--	<0.0005*
Post 1990*Year	<-0.0005*	--	0.072*	--
Post 1995*Year	--	<-0.0005*	--	<0.0005
Constant	1.078***	1.045***	11.672**	19.544**
N	48	48	48	48
F	7.41	3.66	4.91	2.24
P	0.002	0.012	0.002	0.050
R^2	0.25	0.25	0.31	0.22

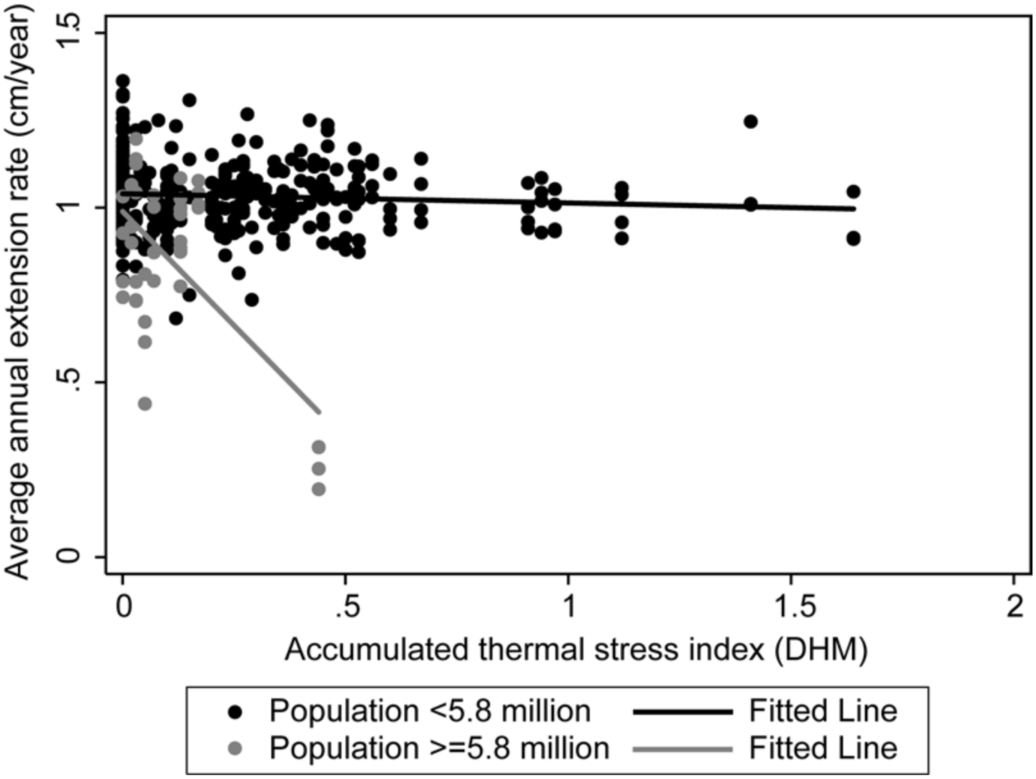


Figure 3-9. **Annual extension for all sites versus DHM from the previous coral-year along with a linear regression on the extension rates that occurred when the human population of Honduras was less than 5.8 million (black) and those that occurred when population exceeded 5.8 million (gray) ($F_{(3,409)}$= 26.92, p< 0.0001, R^2=0.32).** DHM_{t-1} alone is not a significant predictor of extension rates, but the relationship is improved when the effects of population are added.

DISCUSSION

I generated new time series of coral growth over the last century from four sites on the Mesoamerican Reef, utilizing the tree-ring technique of crossdating. These chronologies provide valuable information regarding long-term trends in relative growth rates, the history of coral bleaching, and how both thermal stress and local stressors affect coral growth. In particular, the four chronologies underscore an increase in bleaching frequency over recent years as well as the severity of the 1998 bleaching event. Indeed, ecological surveys dating back to the 1970s confirm that the Mesoamerican Reef experienced its first documented bleaching event in 1995 (Glynn 1993, McField 1999), and a much more severe and widespread bleaching event in 1998 (Kramer and Kramer 2000, McField 2000, Aronson 2002a). Indeed, the 1998 bleaching event was severe and widespread with reports of bleaching around the globe (Spencer et al. 2000, Wilkinson 2000, Bruno et al. 2001, McGrath and Smith 2003, Smith et al. 2008). On the Mesoamerican reef, the 1998 bleaching event was almost certainly unprecedented over the last century as evidenced by a lack of prior stress banding in my cores. Indeed, the 1998 bleaching event may be unprecedented over the last 3,000 years, as shown by exceptional species turnover in coral rubble cores from the Belize lagoon (Aronson et al. 2002b).

Coral bleaching is generally associated with high temperatures and solar irradiation, and indeed thermal stress was exceptional for many locations worldwide where bleaching occurred during 1998 (Lough 2000). However, my calculated DHM, air temperature, and cloudiness records indicate that these variables do not explain the occurrence of mass bleaching on the Mesoamerican Reef in 1998. Warmer temperatures accompanied by higher levels of solar irradiance occurred mid-century, yet no evidence of bleaching could be identified in my samples. Using long-term SST reconstructions, Lough (2000) and Barton and Casey (2005) also found evidence for previous thermal stress comparable to recent levels on the Mesoamerican Reef and in the wider Caribbean. While some SST reconstructions may be affected by data gaps or incorrect spatial interpolation (Barton and Casey 2005), my sites are relatively well-sampled over time (Woodruff et al. 1987). In addition, mid-century warmth is corroborated by high (warm) values of the Atlantic Multidecadal Oscillation, an indicator of climate variability based on Atlantic SST (Kerr 2000), and proxy records of Caribbean SSTs. Coral stable oxygen isotope reconstructions (Gischler and Oschmann 2005, Hetzinger et al. 2008), growth rates from the coral *Siderastrea siderea* from the Bahamas and Belize (Saenger et al. in press), and coral and sclerosponge Sr/Ca records from Florida and Jamaica, respectively (Maupin et al. 2008, Haase-Schramm et al. 2003) all support mid-century warmth that was not accompanied by coral bleaching. This finding that corals on the Mesoamerican Reef did not bleach mid-century despite high thermal stress is consistent with patterns of thermal stress and bleaching in Jamaica. There, underwater ecological observations date to the 1950s, with no reports of mass bleaching until 1987 (Goreau 1992) despite thermal stress in 1957 and 1958 that was comparable to that during the first documented bleaching events in Jamaica (Fig. 3-6).

While heat and solar irradiance stress in 1998 were not exceptional within the past century on the Mesoamerican Reef, local anthropogenic stress has increased in recent decades. Beyond a human population of ~6 million in Honduras, I found that DHM-related declines in extension became greater. Thus, the widespread and severe bleaching event on the Mesoamerican reef during 1998 appears to have resulted from increased local stresses, which lowered coral thermal tolerance and led to bleaching in response to only moderate warming.

Although the relationship between coral extension and local stressors is likely far more complex, the concept that local stress interacts with thermal stress is also consistent with differences in the resistance and resiliency of corals among the four sites. At the Sapodilla Cayes and Utila, long-term decreases in extension rates may be the expression of long-term sublethal stress as these sites. Indeed, Sapodilla and Utila experience higher levels of chronic anthropogenic stress than Cayos Cochinos and Turneffe Atoll (Halpern et al. 2008, Carilli et al. in press). Also, Utila, which experiences high relative chronic stress (Halpern et al. 2008, Carilli et al. in press), is the only site where corals exhibit a significant depression in growth rates and a stress band associated with the 1995 bleaching event. Similar long-term reductions in coral growth rates are not exclusive to the Mesoamerican Reef and have also recently been reported on the Great Barrier Reef (De'ath et al. 2009), in Thailand (Tanzil et al. 2009), and near the Panama Canal (Guzman et al. 2008).

Repetitive bleaching or pre-exposure to high or more variable water temperatures or light may increase a coral's thermal tolerance threshold via acclimatization (Brown et al. 2002, Castillo and Helmuth 2005), offering some potential protection from rising global temperatures. However, the continued acceleration of local stressors such as increased sedimentation through land clearing, marine dredging, and coastal development may depress a coral's energy reserves (Rogers 1990), making it less likely to either resist bleaching or to survive and recover from a bleaching event (Rodrigues and Grottoli 2006). Further observational studies, for instance with extensive in situ instrumentation in place before and during a bleaching event, are needed to identify how specific stressors interact to change the bleaching threshold. Experimental studies might also be useful to calculate the effects of different stressors, such as nutrients or sedimentation, on thermal tolerance thresholds.

These data suggest that chronic local stressors depress the thermal tolerance threshold, increasing the likelihood of coral bleaching under only moderate thermal stress. Though my study addresses *M. faveolata*, the dominant reef framework builder in most of the Mesoamerican reef region, this finding may be common to other coral species and regions (Wooldridge 2009). Therefore, local management strategies that reduce local stressors, such as creating effective marine reserves to protect from overfishing, or reducing runoff impact by watershed management and protecting or replanting coastal mangroves, may increase coral thermal tolerance and thus the associated likelihood of surviving future warming.

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CHAPTER 4: Periodic endolithic algal blooms in *Montastraea faveolata* corals represent periods of low-level stress

ABSTRACT

Cores from the scleractinian coral *Montastraea faveolata* from the Mesoamerican Reef possess obvious green bands, sometimes occurring annually, but more often at less frequent intervals. Bands are remnant concentrations of the endolithic green alga *Ostreobium spp.* that grow parallel to and below the living coral tissue. This study dated green bands in 58 *M. faveolata* cores collected from four sites on the Mesoamerican Reef. We found that the bands are not related to coral growth reductions, but instead are caused by algal blooms within the coral skeleton. We hypothesize that the blooms occur during periods of coral paling, during which more light penetrates into the coral skeleton. This hypothesis is supported by observations of discontinuous banding within the skeleton, the patchiness of pigment loss in living corals, and ecological observations of algal blooms in living bleached corals. At three sites, there was a significant increase in green band occurrence over time, which suggests that coral paling may have increased over the last several decades.

INTRODUCTION

Endolithic algae of the genus *Ostreobium* (Lukas 1974) occur naturally in the skeleton of many coral species, including *Montastraea faveolata*, living just below the tissue layer. Typically, multiple green bands of high endolith concentrations occur throughout the *M. faveolata* coral skeleton (Fig. 4-1A). All green bands except the top band are composed of degrading pigments and are not living (Kanwischer and Wainwright 1967). Although several studies have attempted to explain the existence of green bands of endoliths in coral skeleton, no consensus has been reached. For instance, Odum and Odum (1955) suggested that the endoliths may live in mutualistic symbiosis with the coral, much like zooxanthellae. Lukas (1973) suggested that the endolithic algae grow upwards with the coral, and that during periods of slow coral growth, the algae accumulate into a dense band, with which Le Campion-Alsumard et al. (1995) agreed. Highsmith (1981) instead suggested that bands might represent blooms of endoliths due to improved growth conditions for the algae.

Endolithic algae blooms have been observed under bleached coral tissues in *Oculina patagonica* (Fine and Loya 2002) and *Montastraea faveolata* (Rodríguez-Román et al. 2006). Coral bleaching is a stress response characterized by a reduction in the coral's symbiotic zooxanthellae, or zooxanthellae pigmentation, and on large spatial scales is usually caused by thermal stress (Brown 1997). Other studies have shown that photosynthates synthesized from endolithic production can be translocated to the coral host (Schlichter et al. 1995, Fine and Loya 2002) suggesting that this alternate carbon source might allow some coral species to survive better than others during bleaching events (Fine and Loya 2002, Rodríguez-Román et al. 2006). The loss of pigment from zooxanthellae during bleaching, which normally absorbs >95% of ambient photosynthetically active radiation, can stimulate growth of the endolithic algae due to increased access to light (Fine et al. 2005, Rodríguez-Román et al. 2006). Indeed, under natural bleaching conditions, Fine et al. (2005) found that endolithic algae in *Montipora monasteriata* were able to photoacclimate to increased light, although sudden increases in light did lead to photoinhibition.

We investigated the occurrence of green banding in 58 coral cores from the Mesoamerican Reef which were collected primarily for skeletal growth rate analyses. We find that green bands are not related to coral growth rates, and therefore must occur due to algal blooms. We also show that the occurrence of green bands does not occur randomly, and is increasing over time. These findings suggest that endolithic algae bloom as a result of drivers common to most corals on a reef, instead of intrinsic effects, and that these drivers are increasing. Thus our data provide support for the hypothesis that green bands occur during coral paling, and can therefore be used as proxies for past coral stress.

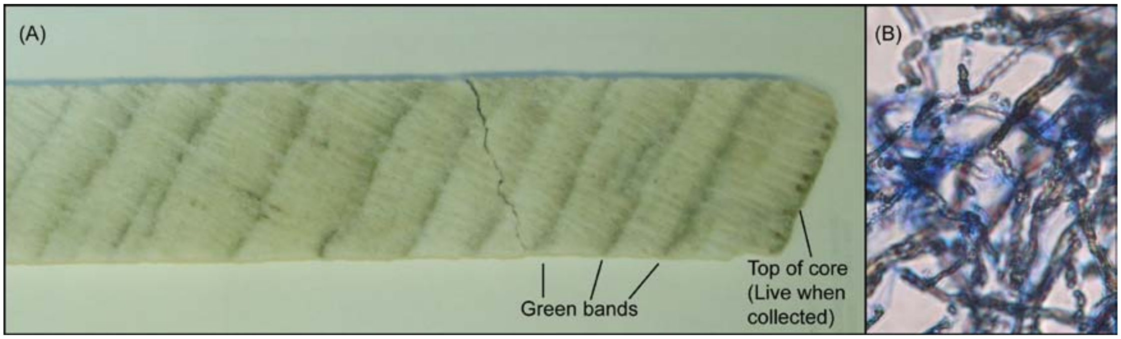


Figure 4-1. (A) Plain light photo of slab removed from core (from the Sapodilla Cayes) showing green bands. (B) Photomicrograph of stained endolithic algae from a decalcified coral sample.

MATERIALS AND METHODS

A total of 92 *Montastraea faveolata* coral cores were collected from 4 sites on the Mesoamerican Reef in 2006 and 2007 (Turneffe Atoll, the Sapodilla Cayes, Utila, and Cayos Cochinos, Fig. 4-2, Table 4-1). Cores were collected between 2.5 and 13 m depth on the fore-reef in spur-and-groove habitat using a hand-held pneumatic drill with a 5 cm diameter core barrel and carbide teeth. Drill holes were filled with pre-cast concrete plugs to facilitate recovery of the coral colonies. Once drilled, the living coral tissue was removed using a water-pik on site and cores were rinsed in fresh water and air-dried. A slab was removed from the middle of each core using a carbide-tipped double-bladed table saw for x-ray analysis. Cores were kept in drawers to deter fading of the green bands, which occurs when algal pigments are exposed to sunlight. Endolithic algae were identified to the genus *Ostreobium* by microscopic inspection of stained decalcified material (Fig. 4-1B).

Coral slabs were x-rayed to reveal annual density banding, which was used to assign dates to green bands (Knutson et al. 1972). 58 cores were chosen for this study based on the clarity of annual bands in their x-rays (14 from Turneffe, 12 from Utila, 10 from Cayos Cochinos, and 22 from the Sapodilla Cayes). Green bands were assigned dates under the assumption that endoliths grow right up against the living coral tissue. In *Porites spp.*, endoliths may grow up to 0.5 cm below the living coral tissue (Le Campion-Alsumard et al. 1995), and this depth may be different for *Montastraea faveolata* but has not yet been quantified. However, skeletal isotopic analyses across green bands indicate that the green bands may form just below the living tissue in *M. faveolata* (Hartmann et al. unpublished data). Time series of green band occurrence were constructed as the percentage of cores with a green band in each individual year (Fig. 4-3). We tested whether the observed proportion of green bands could have occurred due to random change by comparing our data to the Poisson distribution using a chi-squared test. The location of green band occurrence, whether within the high-density or low-density portion of each annual band was also noted. In addition, we quantified the number of bands which were not continuous across a 5 cm wide coral core.

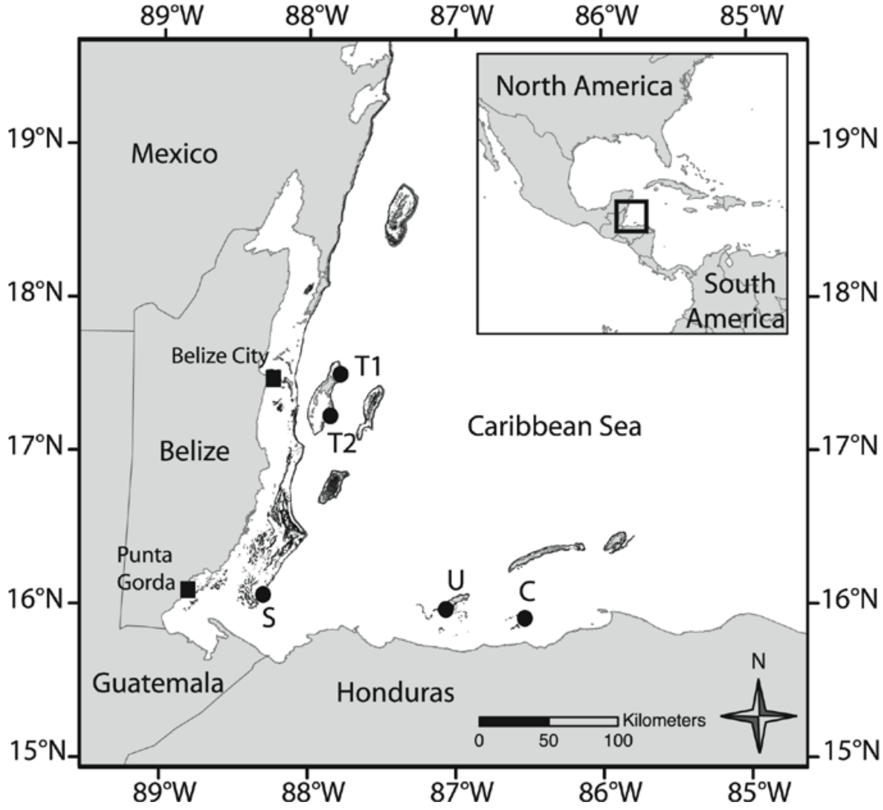


Figure 4-2. Map of the Mesoamerican Reef showing locations of coral collections as black circles. Dark grey denotes coral, light grey denotes land areas. T1, T2 = Turneffe Atoll (4 cores from T1, 13 from T2), S = Sapodilla Cayes, U = Utila, C = Cayos Cochinos.

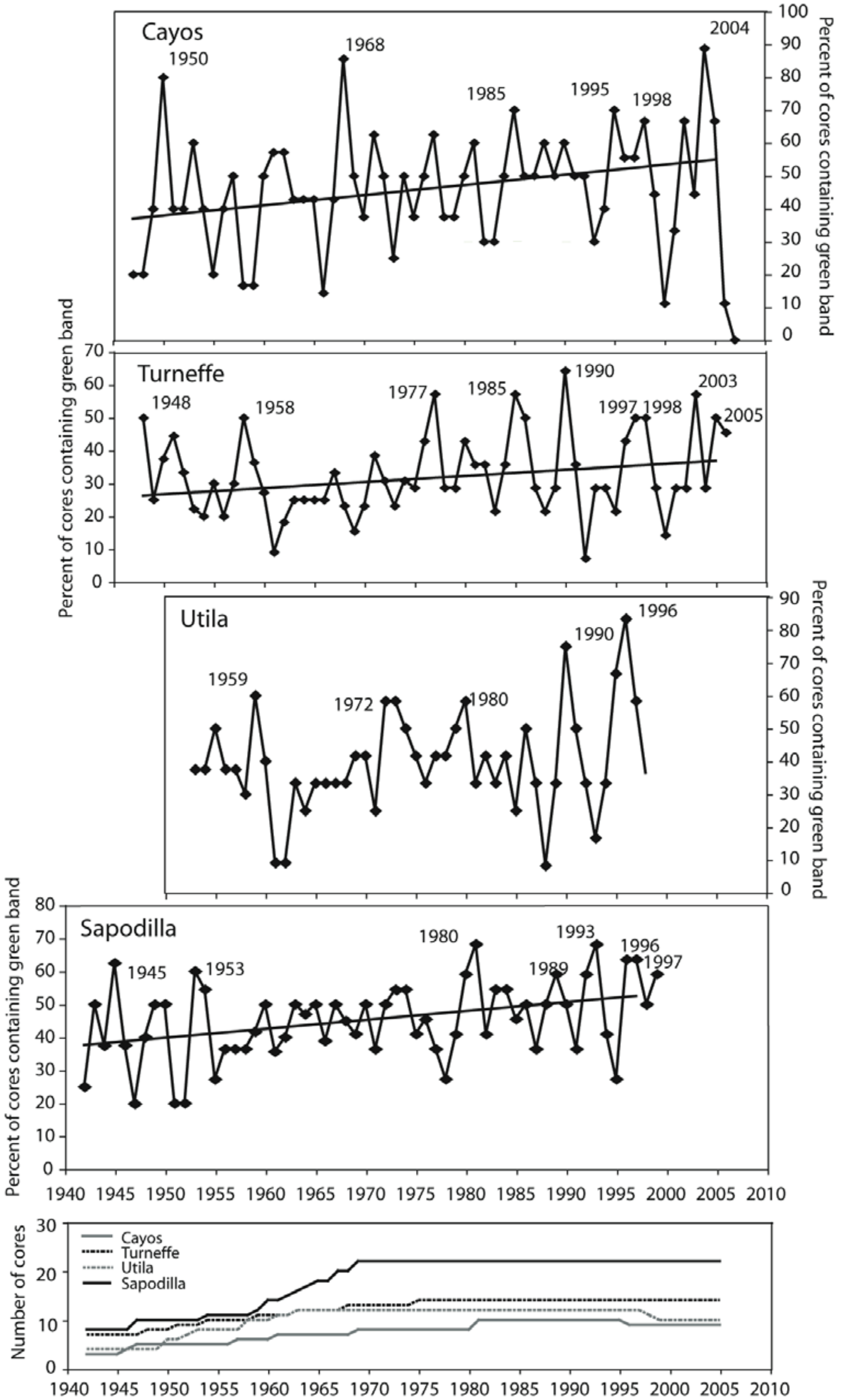
To test whether green bands occur due to periods of diminished coral growth, coral extension rates (cm year^{-1}) and annual density (g cm^{-3} year^{-1}) were separated into two groups: those with a green band and those without a green band. Due to nonnormality of the data, a Mann-Whitney U test was used to test for significant differences in coral growth rates between the green and non-green groups. Note that due to extreme growth suppression in all cores after the 1998 mass bleaching event in corals from the Sapodilla Cayes and Utila, only data through 1997 were used.

Table 4-1. Coral core collection site locations, with dive site name or nearby caye and coordinates.

Site	Dive Site Name	Coordinates
Turneffe 1	Dog Flea Caye	17°29’59” N, 87°45’30” W
Turneffe 2	Harry Jones	17°18’25” N, 87°48’04” W
Sapodilla	Frank’s Caye, Northeast buoy	16°07’45” N, 88°14’59” W
Utila	Diamond Caye	16°03’52” N, 86°57’30” W
Cayos Cochinos	Pelican Point, Peli 2	15°58’41” N, 86°29’06” W

Logistic regression analysis was used to determine whether there was a significant change in the probability of green band occurrence over time. First, a linear model was used to describe the probability of green band occurrence with time. The best-fit parameters of the model were then estimated using the Nelder-Mead optimization algorithm. A likelihood ratio test was used to determine whether the slope for the model was significantly different than zero.

Figure 4-3 (facing page). Percentage of cores from each site with green bands in a given year (diamonds), and fitted values from the logistic regression model (black line). For clarity, chronologies are plotted with at least 8 cores, except for Cayos Cochinos, which is shown with at least 5 cores. Bottom panel: the number of cores comprising each chronology above.


Cayos
1950
1968
1985
1995
1998
2004
100
90
80
70
60
50
40
30
20
10
0
Percent of cores containing green band
Turneffe
1948
1958
1977
1985
1990
1997
1998
2003
2005
70
60
50
40
30
20
10
0
Percent of cores containing green band
Utila
1959
1972
1980
1990
1996
90
80
70
60
50
40
30
20
10
0
Percent of cores containing green band
Sapodilla
1945
1953
1980
1989
1993
1996
1997
80
70
60
50
40
30
20
10
0
Percent of cores containing green band
1940
1945
1950
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
Number of cores
30
20
10
0
Cayos
Turneffe
Utila
Sapodilla
1940
1945
1950
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010

RESULTS

A total of 774 green bands were identified in the samples used for this study. There was no significant difference in coral extension or density in years with or without green bands (Fig. 4-4, Mann-Whitney U test, p=0.44 and 0.11, respectively). In our sample set, 64% of the bands were found within the high-density portion of a skeletal band. 11% of the green bands identified were discontinuous across the 5 cm width of the cores and either ended partway across a core or shifted abruptly to a slightly different depth in the core.

Within each core, the mean proportion of years with a green band out of all total years at all sites was 0.26 ±0.09 (mean ±SD), and there was a significant difference between the occurrence of green bands at Turneffe Atoll (0.18 ±0.06) and the Sapodilla Cayes (0.26 ±0.08) (p= 0.004, Mann-Whitney U test).

Time series of the occurrence of green bands for all the cores from a given site show that some years have a higher incidence of cores with green bands than others, and that the distribution of green bands is not random ($p<0.001$, Chi-squared test). Some of these common years are shared between sites, such as 1980 and 1985, but some years with high green band incidence only occur at a single site, such as 2004 (Fig. 4-3). The logistic regression determined that the proportion of cores containing a green band increased over time both among all sites pooled and within all individual sites aside from Utila (Fig. 4-3). The oldest core in our sample set extends back to 1869, and includes a green band in that year.

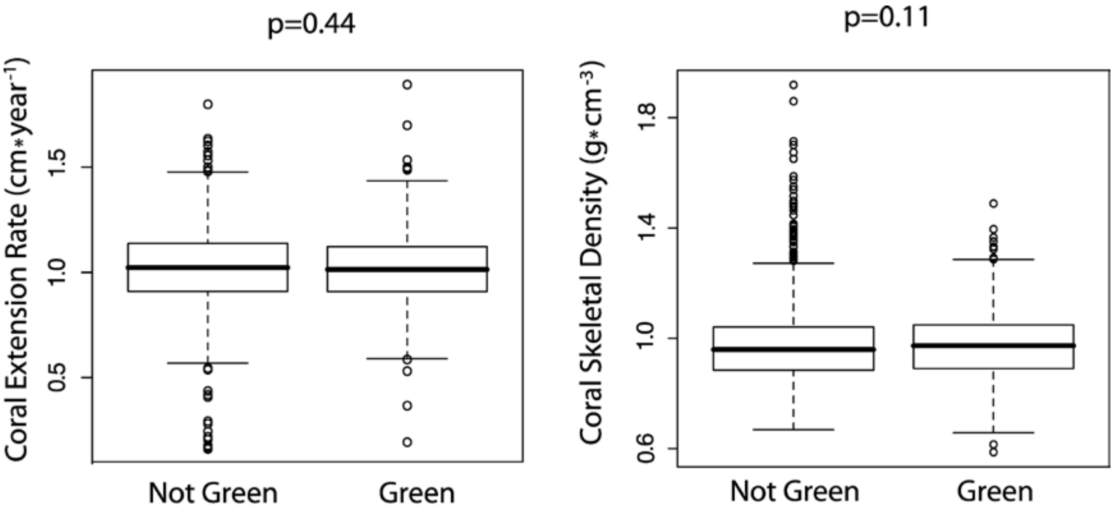


Figure 4-4. Boxplots of skeletal extension and density for years without green bands and years with green bands. There is no significant difference in either parameter during years with or without a green band (p-values calculated by the Mann-Whitney U test).

DISCUSSION

We find no significant relationship between coral growth rates and the occurrence of green banding. Therefore, the occurrence of green bands must occur as a result of algal blooms. Other studies have shown that endolithic algae bloom under bleached coral tissues (Fine et al. 2002, Rodríquez-Román et al. 2006). The lack of widespread occurrence of green bands during known years of mass coral bleaching, however, indicates that green bands are not a simple proxy for coral bleaching per se. Severe, large-scale bleaching events occurred on the Mesoamerican Reef during the summer of 1995 (McField 1999) and 1998 (McField 2000). However, coral cores from the Sapodilla Cayes and Utila do not have a high incidence of green bands in these years, and Turneffe Atoll cores only have a high incidence of green bands during 1998, not 1995. In addition, we find green bands deep in the coral cores, some of which are as old as 1860, but no large-scale bleaching was reported on the Mesoamerican Reef until the 1990's.

Fine et al. (2005) showed that endolithic algae become photoinhibited when exposed quickly to increased light, but that during slow loss of zooxanthellae, the endoliths were able to photoacclimate and continue photosynthesis. These authors suggested that more resistant corals, which may take longer to bleach, could allow photoacclimation of the endolithic algae. Since *Montastraea faveolata* is one of the first corals to show signs of bleaching (Fitt and Warner 1995), during severe bleaching years, the loss of zooxanthellae may be so rapid that the endolithic algae are not able to photoacclimate, and no bloom occurs. *M. faveolata* normally experiences seasonal fluctuations in zooxanthellae and chlorophyll-a density, even during years not recognized as a bleaching event (Fitt et al. 2000). Our data shows that green bands are common in Mesoamerican *M. faveolata*, suggesting that the process forming bands is not extraordinary and that the bands do not represent severe perturbations to normal coral growth.

Patchy endolith blooms within a coral head are indicated by the discontinuous nature of some green bands (11% of the bands observed here). *Montastraea faveolata* tends to experience patchy paling or bleaching on its upper surfaces, attributed to differential loss of zooxanthellae *Symbiodinium* clades with low thermal susceptibility (Rowan et al. 1997, Fig. 4-5). The observations of some very old green bands, an increase in green band occurrence over time, the discontinuous nature of some green bands, and ecological observations of patchy and frequent paling in *M. faveolata*, suggest that the green bands in *M. faveolata* may be used as a proxy for past paling, or low-level bleaching (Fig. 4-5), but do not represent periods of complete bleaching.

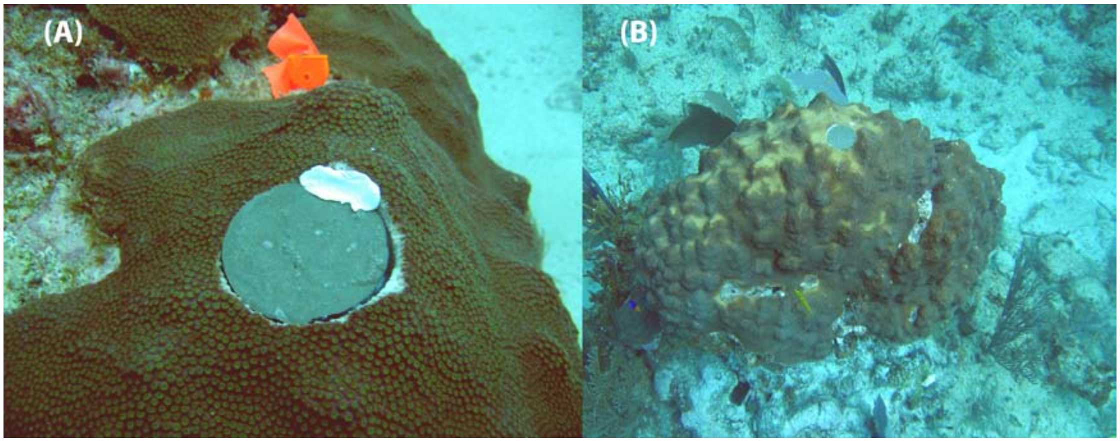


Figure 4-5. (A) *Montastraea faveolata* colony with normal pigmentation. (B) *M. faveolata* colony with significant paling on the top surfaces.

The between-site differences in years with a high proportion of cores with a green band indicate that local-scale instead of regional-scale forcing factors are driving the endolithic algae blooms. These sites experience a range of local stressors, with land-based runoff highest at the Sapodilla Cayes, followed by Cayos Cochinos, Utila, and Turneffe Atoll (Prouty et al. 2008). Recent work has shown that corals experiencing increased local stress such as runoff are more susceptible to bleaching (Wooldridge et al. 2009) and recover to normal growth rates more slowly after bleaching (Carilli et al. in press). Of the sites studied here, a metric of stress on reef communities involving quantitative assessments of local human population size, fishing pressure and both sediment and nutrient runoff demonstrated that Turneffe Atoll experiences the lowest level of local stress (Carilli et al. in press). Indeed, Turneffe also has the lowest overall levels of green band occurrence. We suggest that spatial differences in background stress contribute to between-site differences in the frequency and timing of paling and green band formation. Our findings suggest that green bands can be used as a proxy for coral paling, or generalized coral stress.

Even excluding the period since the globally and regionally severe bleaching event in 1998, we find a statistically significant trend toward increasing frequency of green banding toward the present. If we assume that green bands can be used as a proxy for coral paling, this trend suggests that paling has increased over the past century, possibly pointing to an overall increase in low level stress within Mesoamerican *Montastraea faveolata*. We speculate that the increased incidence of paling may reflect the overall history of stress on reef corals hosting endolithic algae better than does the occurrence of severe bleaching events or periods of partial mortality.

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CHAPTER 5: Century-scale records of land-based activities recorded in Mesoamerican coral cores

ABSTRACT

The Mesoamerican Reef, the second-largest barrier reef in the world, is located in the western Caribbean Sea off the coasts of Mexico, Belize, Guatemala, and Honduras. Particularly in the south, the surrounding watersheds are steep and the climate is extremely wet. With development and agricultural expansion, the potential for negative impacts to the reef from land-based runoff becomes high. I constructed annually resolved century-scale records of metal/calcium ratios in coral skeletons collected from four sites experiencing a gradient of land-based runoff. My proxy data indicate that runoff onto the reef has increased relatively steadily over time at all sites, consistent with land use trends from historical records. Sediment supply to the reef is greater in the south, and these more exposed reefs will probably benefit most immediately from management that targets runoff reduction. However, because runoff at all sites is steadily increasing, even distal sites will benefit from watershed management.

INTRODUCTION

Land use in Mesoamerica is following the trajectory seen in many locations worldwide: as population increases, development increases and agricultural areas expand into native habitat (Fig. 5-1). Agricultural intensification and development are usually associated with increased erosion and sediment-laden runoff (Matson et al. 1997). Land-use change tends to increase both the amount of freshwater runoff and the sediment content of that runoff (Foley et al. 2005). Indeed, Burke and Sugg (2006) modeled runoff between natural land cover and the altered land cover in the watersheds surrounding the Mesoamerican Reef in 2004, and found a doubling of overall freshwater runoff and a 20-fold increase in the amount of sediment eroded, as well as much higher levels of nutrient runoff as well. Here I use the term runoff to encompass both of these possible scenarios (an increase in the total amount of freshwater discharge and an increase in the amount of contaminants in that discharge), which are not mutually exclusive. Burke and Sugg (2006) also showed that the majority of sedimentation and nutrient runoff in the region originates in Honduras, while Kok (2004) showed that agricultural expansion of many products in Honduras is concentrated in watersheds draining into the Gulf of Honduras. Therefore, I would expect runoff impacts to the reef to be higher in the south, and to have increased over time.

Runoff from land can have deleterious effects on corals. Sediment particles may smother and abrade the coral animal, and suspended matter reduces light incidence and photosynthesis in the coral’s algal symbionts (Dodge and Vaisnys 1977, Rogers 1990). Sedimentation can lead to reduced skeletal growth rates (Dodge and Vaisnys 1977), reduced fecundity (Kojis and Quinn 1984), and changes in community structure (Rogers, 1990). Heavy metal pollution from runoff is also a concern for corals. For instance, Negri and Heyward (2001) found that copper and tributylin inhibit fertilization and larval metamorphosis in *Acropora millepora*, and Richmond (1993) and Peters et al. (1997) both reviewed several studies that found negative effects due to metal exposure, including coral bleaching (the loss of symbiotic algae) and death. Coral health in Mesoamerica has recently declined, as shown by growth rates (Carilli et al. in review) and ecological surveys (McClanahan et al. 1999; McField 1999). Therefore, I was interested in investigating the link between coral reef health and changes in runoff as documented in both historical records and coral proxy records recovered from geochemical time-series.

I used drill cores from massive corals heads to document temporal trends in runoff to the reef system. Scleractinian corals can live for hundreds of years and continuously record changes in the marine environment in their aragonitic skeletons. Annual density banding in corals allows accurate time control on reconstructions (Knutson et al. 1972), and many studies have utilized corals for paleoclimatic and paleoenvironmental reconstruction, measuring stable isotopes (Dunbar et al. 1994, Cobb et al. 2003, Marion et al. 2005) and metals that substitute into the $CaCO_3$ matrix (Smith et al. 1979, Hanna and Muir 1990, Bastidas and Garcia 1999, Fallon et al. 2002, David 2003, McCulloch et al. 2003, Ramos et al. 2004, Fleitmann et al. 2007, Lewis et al. 2007, Prouty et al. 2008). Although the coral calcification mechanism and therefore the exact pathway of metal substitution in the aragonite matrix are still under debate (Cohen and McConnaughey 2003), empirical studies have shown that corals appear to faithfully record relative metal concentrations in the surrounding seawater (Runnalls and Coleman 2003, Correge 2006).

In this paper I extend the temporal records of seven metals that Prouty et al. (2008) found to be well suited as indicators of environmental change in *Montastraea faveolata* from four sites on the Mesoamerican Reef: Turneffe Atoll, the Sapodilla Cayes, Utila, and Cayos Cochinos (Fig. 5-2). Here I present annually-resolved, century-scale records of Ba/Ca (barium), Mn/Ca (manganese), Cr/Ca (chromium), Sb/Ca (antimony), Cu/Ca (copper), Pb/Ca (lead) and Zn/Ca (zinc). My sites span a gradient of hypothesized land-based influence, with higher runoff impacts in the south and lower impacts towards the north and farther from land (Burke and Sugg 2006, Chérubin et al. 2008). Records of trace metal variation were constructed over the past 100-150 years to investigate how land-based runoff has changed over this time period. In addition, water samples were collected from offshore transects and all metals were analyzed and compared to maps of chlorophyll-a to investigate spatial patterns related to coastal runoff.

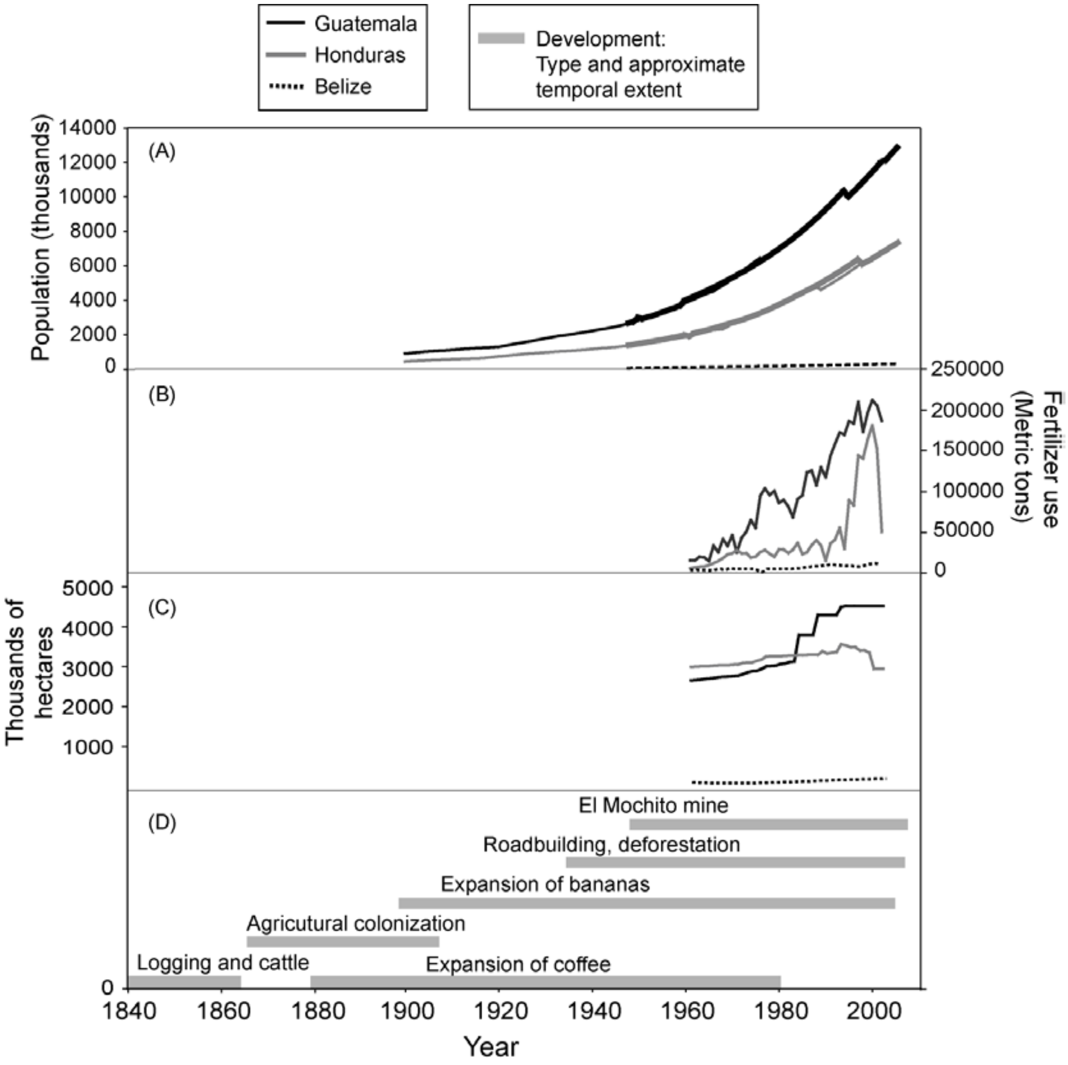

Figure 5-1. Time series of population and development in Guatemala, Honduras, and Belize. (A) Population of each country, from the United Nations (2006) (thick line) and the Oxford Latin American Economic History Database (2009) (thin line). (B) The amount of fertilizer used in each country. (C) The amount of land used for agriculture in each country. (B) and (C) show data from the Food and Agriculture Organization of the United Nations (2004). (D) Labeled gray bars show approximate time period during which a particular form of development or land use was occurring in the region. These time periods are from Hall and Brignoli (2003).

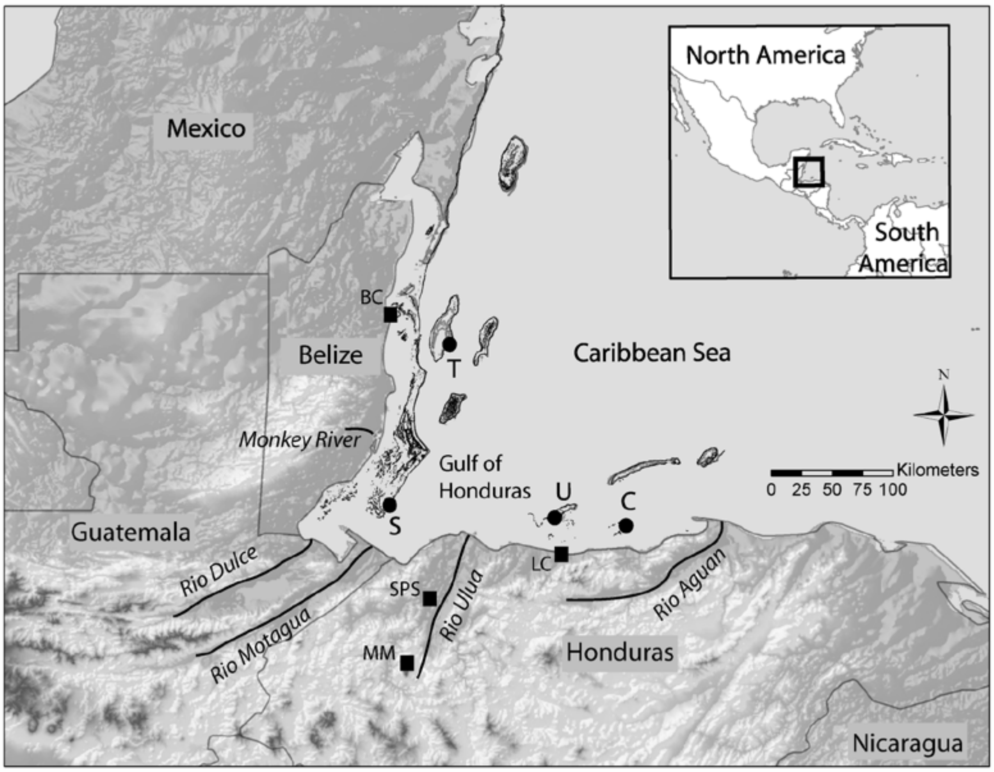

Figure 5-2. Topographic map of the Mesoamerican Reef region. Reef areas are in dark gray. Coral collection sites are marked with black circles. T = Turneffe Atoll, S = Sapodilla Cayes, U = Utila, and C = Cayos Cochinos. Rivers are denoted with black lines and named in italics. Landmarks are denoted with black squares. BC= Belize City, PB = Puerto Barrios, SPS = San Pedro Sula, MM = El Mochito Mine, LC = La Ceiba.

BACKGROUND

The selected metals are indicators of a variety of land-based sources ranging from terrigenous sedimentation to mining waste. Coral Ba/Ca ratios have been used as tracers of sediment runoff, since Ba desorbs from terrigenous particles when fresh and saltwater mix (Alibert et al. 2003, McCulloch et al. 2003, Fleittman et al. 2007). Mn tracks primary productivity, which would be influenced by nutrient delivery from rivers and therefore also reflect variations in terrestrial runoff (Abram et al. 2003, Alibert et al. 2003). The other metal/Ca ratios can also indicate impacts due to land-based activities. For instance, Fallon et al. (2002) used coral records of Zn, Pb, and Mn and David (2003) analyzed Cu, Mn, and Pb to investigate runoff from mines adjacent to coral reefs. In the Mesoamerican Reef, Prouty et al. (2008) found higher Sb/Ca and Cu/Ca ratios in coral samples collected from the Honduran sites, suggesting that these elevated concentrations may be due to copper-antimony antifouling paint used on industrial and recreational ships in the Gulf of Honduras. They also suggested that Pb/Ca and Zn/Ca ratios, which were elevated at Utila compared to other sites, may represent the influence of runoff from El Mochito mine, the largest Pb/Zn mine in the region, via the Rio Ulua that drains into the Gulf of Honduras.

MATERIALS AND METHODS

Coral Collection

M. faveolata cores were collected from four sites on the Mesoamerican Reef: Turneffe Atoll and the Sapodilla Cayes in Belize, and Utila and Cayos Cochinos in Honduras (Fig. 5-2). Cores were collected vertically using a 5-cm diameter stainless steel and brass core barrel with carbide cutting teeth driven by a reversible air-powered drill. Tissue was removed using a water-pik and cores were rinsed in freshwater and air dried. Upon return to Scripps Institution of Oceanography (SIO) in La Jolla California, an 8-mm thick slab was removed from the middle of each core section using a carbide-tipped double-bladed table saw lubricated with freshwater.

Slabs were x-rayed at Thornton Hospital to reveal annual density banding (Knutson et al., 1972). One core from each site was chosen to construct annual-scale time series of metal contamination, assuming local-scale homogeneity (e.g., colony and reef scale) for the given element analyzed (Prouty et al., 2008).

Sample Preparation

Digital x-rays were printed and taped to each core to guide sampling of individual year-bands (average annual extension rate is about 8 mm). A band saw with a thin (~0.5 mm wide) steel blade was used to cut annual blocks along the length of each core, from the top of one annual high-density band to the top of the next. The high-density skeleton tends to form in late summer-fall in *M. faveolata* in this region (Cruz-Piñón et al. 2003) and therefore each annual band represents approximately October of one year to September of the next year.

Standard trace-element protocols for cleaning Teflon labware and preparing samples for analysis were conducted in a class-100 clean room at SIO (initial cleaning) and Woods Hole Oceanographic Institution (WHOI) in Woods Hole Massachusetts (sample analysis). Coral samples were cleaned to remove surface contamination and non-aragonitic-lattice bound phases using a method modified from Shen and Boyle (1988), Guzman and Jarvis (1996) and Bastidas and Garcia (1999). The pre-cleaning procedure involved a coarse crush, ultrasonicating three times at 10-minute intervals in quartz-distilled MilliQ 18 MΩ deionized water. All cleaning solutions were prepared using this ultra-clean water. Samples were next leached in

0.015 N HNO_3 for 20 minutes. The cleaning procedure included a sequence of oxidizing, reducing, and leaching steps with multiple rinses and ultrasonication between. Finally, samples were dried and homogenized using an agate mortar and pestle and sieved with a polypropylene sieve to assure that the particle size was less than 700μm. Powdered samples were stored in acid-washed polypropylene vials until analysis at WHOI.

Sample Analysis

Prior to analysis, approximately 1 mg of homogenized coral aragonite powder was weighed out and dissolved in 4 ml 2% Seastar ultrapure HNO_3 spiked with 0.1 ppb of an indium (In) standard using MilliQ 18 MΩ deionized water. Samples were dissolved in clean Teflon vials for at least 12 hours on a shaker table to maximize carbonate dissolution. This dilution yielded a Ca concentration of approximately 100 ppm to minimize between-sample differences associated with matrix-induced mass discrimination (Rosenthal et al. 1999). The In spike served as an internal standard to facilitate corrections of instrument drift and sample matrix effects. Typical sensitivity was ~1 x 10^6 counts per second per 0.1 ppb In. Analytes were pipetted to 0.5 ml Teflon vials for analysis. Trace element analysis was conducted using a Finnigan Element2 high-resolution double focusing magnetic sector-field inductively coupled plasma mass spectrometer (HR-SF-ICP-MS) at WHOI. Details regarding sample analysis can be found in Prouty et al. (2008). The limits of detection (LOD) were calculated as three times the standard deviation of the counts per second of the blanks

(Zacherl et al. 2003). I calculated the average signal strength as LOD % for my samples by computing the ratio of the average unknown and external and internal standard counts per second to the LOD for each metal (Table 5-2).

Table 5-1. Standard error for each metal/Ca ratio.

Metal/Ca	Standard Error ±
Ba/Ca	3.15×10^5
Cr/Ca	8.18×10^5
Cu/Ca	5.17×10^6
Mn/Ca	5.05×10^5
Pb/Ca	3.94×10^6
Sb/Ca	1.28×10^6
Zn/Ca	2.43×10^5

Table 5-2. The average signal strength of each element expressed as a percentage of the limits of detection.

Element	LOD %
Ba	45,497
Ca	973,789
Cr	912
Cu	1,350
Mn	3,622
Pb	2,051
Sb	907
Zn	3,020

Seawater Samples

Seawater samples were collected from 0.5 m depth for metal/Ca analysis on two transects from Cayos Cochinos towards the coastline (Fig. 5-3). Four samples were collected on each transect and were filtered with 0.7 µm glass fiber filters to remove suspended solids. The filtrate was collected in 500 ml acid-washed polyethelene bottles and stored refrigerated and non-acidified until analysis for metal/Ca.

Seawater samples were diluted in a 1:20 seawater: 2% Seastar HNO_3 ratio and spiked with 0.1 ppb In. An aliquot of one sample was used to add a multi-element standard in multiple concentrations from 5-200 ppm. Analytes were pipetted to 0.5 ml Teflon vials for analysis. Seawater samples were run in the following sequence: alternating single unknowns and blanks, then alternating multi-element solution standards and blanks.

Chlorophyll-a Concentrations

Chlorophyll-a may reflect the influence of nutrients delivered from coastal runoff in non-upwelling regions (Furnas et al. 2005). Therefore, differences in chlorophyll-a concentrations between sites were compared using monthly-averaged satellite-derived data spanning October 1997 to October 2007, obtained from the Sea-viewing Wide Field-of-view Sensor (Sea-WiFS) from NOAA Coastwatch (O'Reilly et al. 1998). The mapped monthly averages from June 16th-July16th 2007 were also obtained from SeaWiFS to compare to seawater samples, which were collected during that time period.

Data Analysis

Coral metal/Ca ratios are non-normal and no transformation satisfied the assumption of normality. Statistical tests were performed using R software (R Core Development Team 2005). Metal/Ca ratios were tested for significant differences between sites using pairwise permutation tests. To investigate temporal trends at each site, data were smoothed using a kernel smoother with a bandwidth of 50 years, and then a linear model was fit to the smoothed data to determine if year was a significant predictor of the smoothed metal/Ca. I also binned data into decades and calculated the median value. I also tested for trends in these decadal medians by fitting a linear model to those data.

RESULTS AND DISCUSSION

Seawater

Both transects show decreasing Ba/Ca with distance from the coast (Fig. 5-3C). Transect T, from near the mouth of the Aguan towards the west, has the steepest slope as well as the highest concentration at the second sampling site. Mn/Ca seawater concentrations (not shown) have a similar pattern to Ba/Ca. The chlorophyll-a concentrations during the month of seawater sample collection were highest near the coast and decreased away from land (Fig. 5-3A), indicating that land-based runoff provides nutrients in this region needed to stimulate algal growth. Seawater Ba/Ca and Mn/Ca also have a similar pattern to the chlorophyll-a concentrations (Fig. 5-3). The pattern of decreasing Ba/Ca and Mn/Ca with distance from the coast and similarity with the chlorophyll-a concentrations is consistent with the idea that these metal/Ca ratios represent fluvial runoff enriched in terrestrial sediment and nutrients.

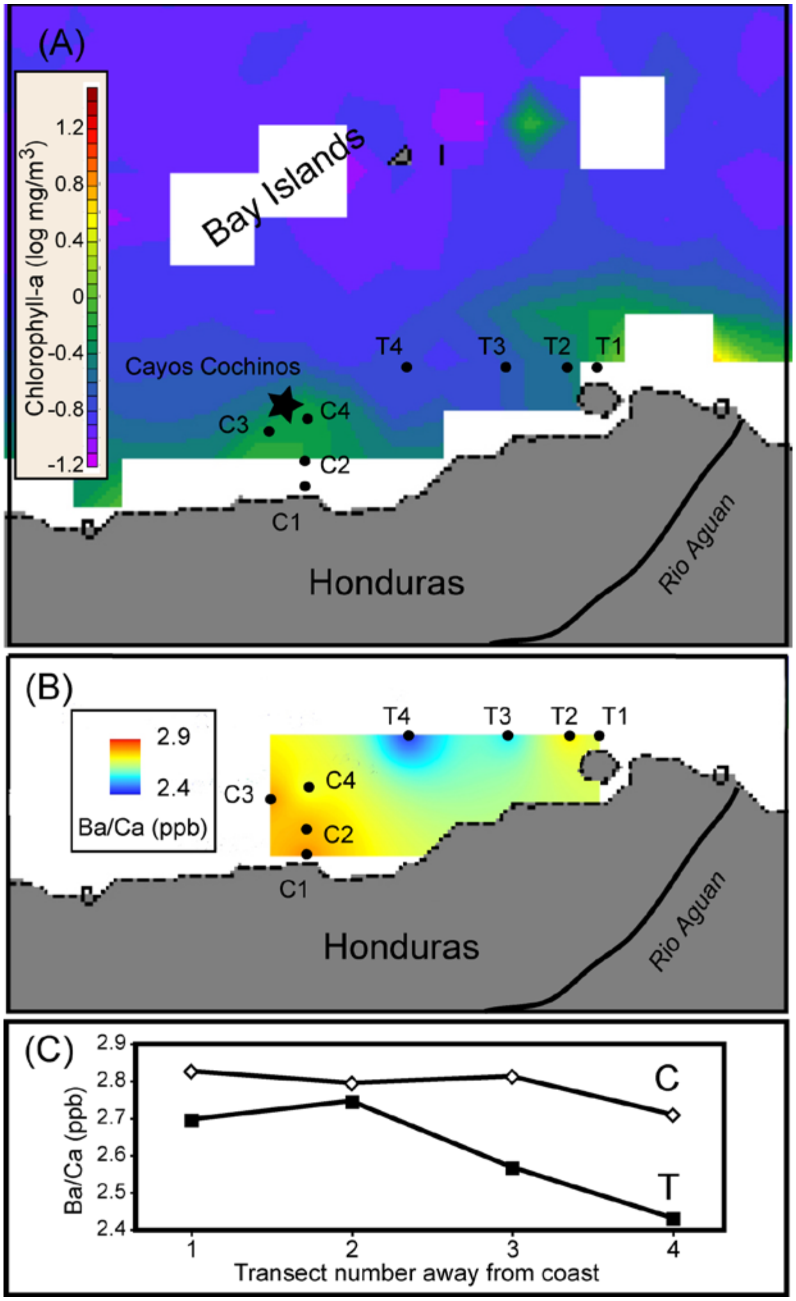

Figure 5-3. Comparison between SeaWiFS-derived chlorophyll-a and seawater Ba/Ca measurements. (A) Monthly composite chlorophyll-a from SeaWiFS on the 16th of July 2007, along with seawater sampling sites on two transects, C and T, between Cayos Cochinos and the Honduran mainland. Seawater samples were collected on the 13th and 14th of July, 2007. (B) Contour plot of Ba/Ca.(C) Ba/Ca from all eight seawater sampling sites on transects C and T.

Coral Samples

Overall differences in metal concentrations between sites through time preserve the same rank order as in the replicate core-top samples observed by Prouty et al. (2008), with Turneffe consistently having the lowest levels of metals (Fig. 5-4, 5-5). Sapodilla Cayes has the highest influence from terrestrial runoff based on Ba/Ca ratios, followed by Cayos Cochinos, Utila, and Turneffe Atoll. Sapodilla Cayes also has the highest levels of Sb/Ca compared to all other sites. For several metals, there is no statistical difference between the Sapodilla Cayes and Cayos Cochinos, but both of these sites are enriched in Cr/Ca, Cu/Ca, Mn/Ca, Pb/Ca, and Zn/Ca compared with Utila and Turneffe, which are not significantly different from one another for Pb/Ca and Zn/Ca (Table 5-3). These rankings, with higher runoff affecting the sites in the south (Sapodilla, Utila, and Cayos Cochinos), and those closest to land (Sapodilla and Cayos Cochinos) agree with average chlorophyll-a concentrations (Fig. 5-5), and also the expected pattern of the highest metal/Ca ratios at sites closest to the main sources of runoff in Honduras (Burke and Sugg 2006, Chérubin et al. 2008).

Figure 5-4. Long term records of metals. (A) Annual metal/Ca at each site in μmol/mol. (B) Medians of decadal bins of metal/Ca at each site in μmol/mol. Note different scales on axes.

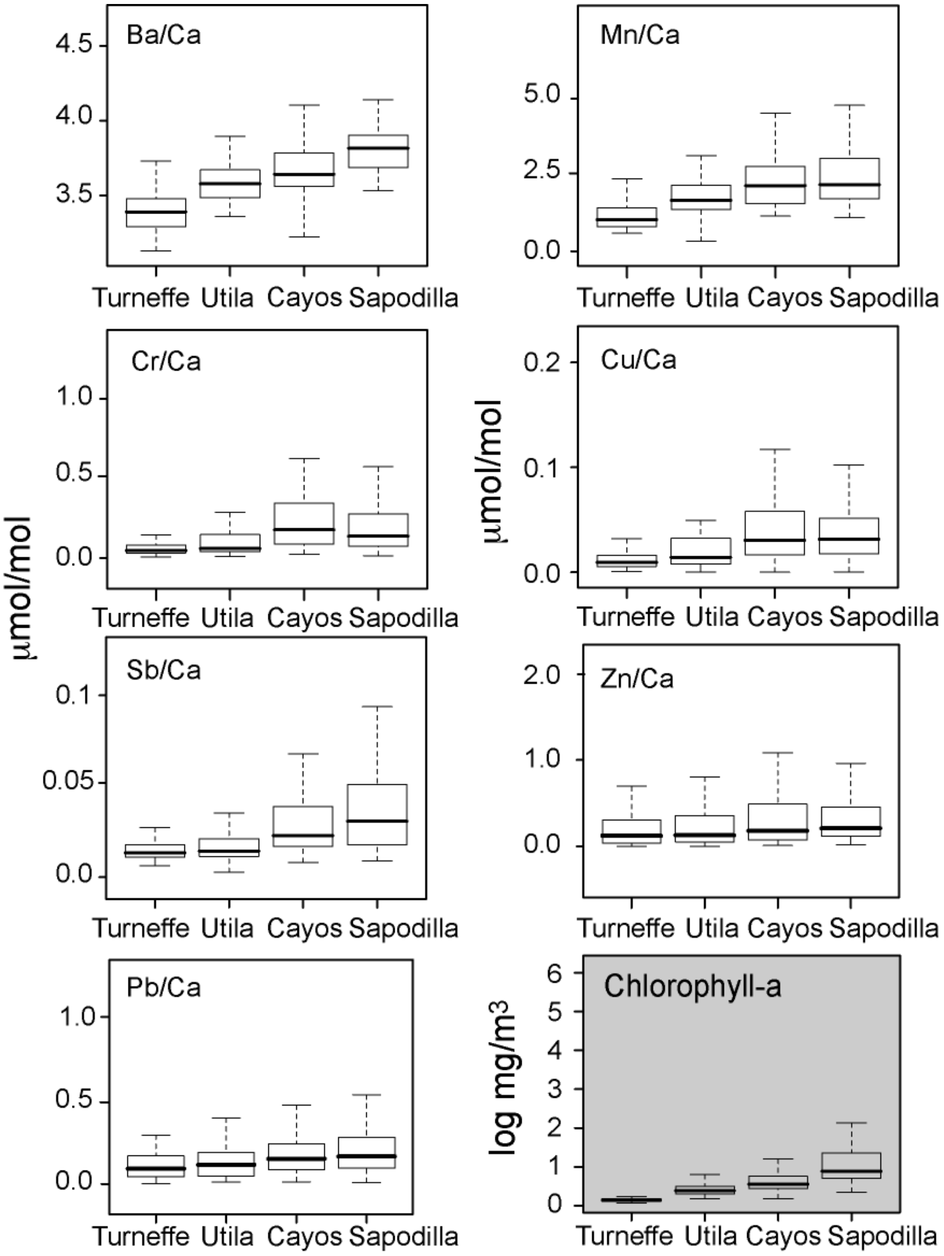

Figure 5-5. **Boxplots of metal/Ca at each site over the length of each record as well as chlorophyll-a from SeaWiFS. Note that outliers have not been plotted. Note also that records span different lengths of time (Turneffe: 1892-2005, Utila: 1907-2005, Cayos Cochinos: 1844-2006, Sapodilla: 1901-2006, chlorophyll-a: 1997-2007).**

Table 5-3. Metal/Ca ratios that are significantly different ($p<0.05$) between sites as tested using pairwise permutation tests.

Sites	Turneffe	Utila	Cayos Cochinos	Sapodilla
Turneffe	--	Ba, Cr, Cu, Mn, Sb	Ba, Cr, Cu, Mn, Pb, Sb, Zn	Ba, Cr, Cu, Mn, Pb, Sb, Zn
Utila		--	Ba, Cr, Cu, Mn, Pb, Sb	Ba, Cr, Cu, Mn, Pb, Sb, Zn
Cayos Cochinos			--	Ba, Sb

Metals that have significant ($p<0.05$) increasing baseline trends, based on both smoothed and binned data, are noted in Table 4. Ba/Ca increases over time at all sites, indicating that sediment delivery to the reef has increased over the past 100-150 years, and this increase appears to have been steady (Fig. 5-4), similar to increases in land use and development adjacent to the reef (Fig. 5-1). All other metals have increasing trends at one or more sites. However, although the rank difference between sites is maintained, not all metals have increasing trends. Note that the large peaks in some metals throughout the records may stem from actual large pulses of contaminated runoff, sampling intermittent particles enriched in a particular metal, or analytical noise associated with high limits of detection in relation to the metal abundance. Therefore, instead of interpreting individual peaks, I focus my interpretation on the trends of the metal baselines calculated from either smoothed or binned data as these time-series are more robust to statistical analysis, (Table 5-4 and Fig. 5-4b).

Table 5-4. Metal/Ca ratios that have significant ($p<0.05$) increasing trends at each site. "Median" shows metals for which trends are significant, as tested by fitting a linear model to the medians of data binned by decade. For Sapodilla and Utila, the decade 1900 was excluded for all tests except Ba/Ca. "Smoothed" shows metals for which trends were significant as tested by smoothing data with a kernel filter (bandwidth 50) and fitting a linear model to the smoothed dataset.

Site	**Turneffe**	**Utila**	**Cayos Cochinos**	**Sapodilla**
Median	Ba, Pb	Ba, Mn*	Ba	Mn, Cu, Sb*
Smoothed	Ba, Cr, Sb	Ba, Cr, Mn	Ba	Ba, Cu, Sb, Zn

*$p<0.06$

Records of river discharge and rainfall for the region are somewhat sparse in both space and time. Monthly average river discharge from gauge stations along three major rivers in Honduras (the Ulua, Chamelecon, and Aguan) are plotted in Fig. 5-6. The longest rainfall records for the region, from Belize City and Guatemala City, are also plotted for comparison (Fig. 5-6). A thorough investigation of trends in the climatology and hydrology of this region is beyond the scope of this study, however simple linear regressions through each of these records indicates a lack of consistent trends: about half of the river discharge records have an increasing trend, while half have a decreasing trend. Similarly, rainfall at Guatemala City has a decreasing trend, while that at Belize City has an increasing trend. However, the large amount of annual rainfall (regional average ~200 cm), and relatively small interannual variability (standard deviation ~30 cm) suggest that these trends are probably insignificant. My metal/Ca records may instead be more robust measures of overall runoff affecting the Mesoamerican Reef, as these records average runoff impacts over both time and space, as opposed to the river discharge and rainfall measurements which may contain biases due to unrepresentative catchment behavior.

Chérubin et al. (2008) modeled the advection of runoff plumes across the Mesoamerican Reef. They found that runoff mainly originated from Honduras, but plumes were advected in a counterclockwise gyre around the reef. This mixing of runoff over the reef may explain the similar trends in Ba/Ca across sites: the runoff is all originating from the same location, but the signal is diluted with greater distance from the main source: the Gulf of Honduras. The other metals may be more affected by localized conditions, such as scavenging by particles or biological activity.

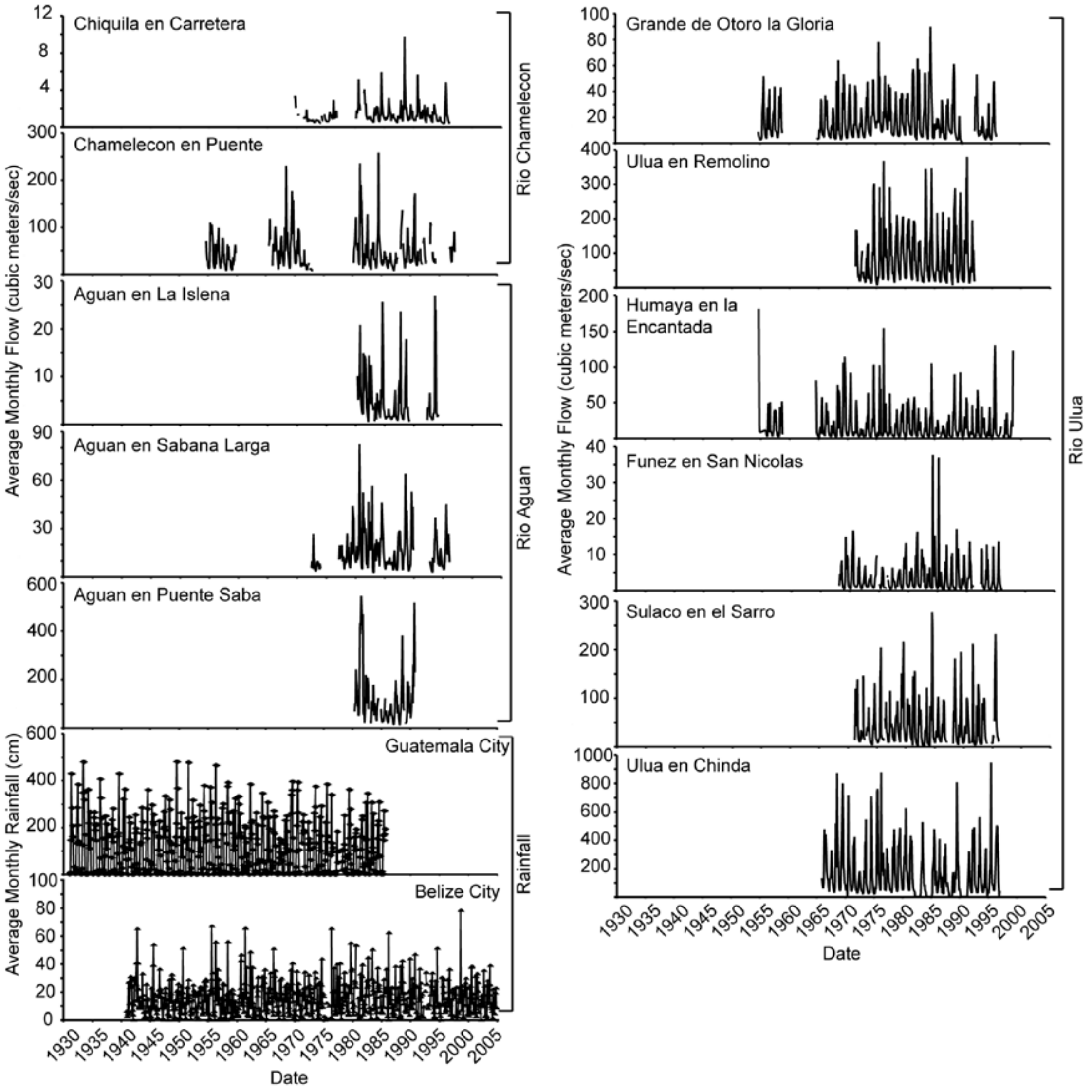

Figure 5-6. Monthly average river discharge (cubic meters/second) at various gauging stations on three major rivers in Honduras, the Ulua, Chamelecon, and Aguan, provided by C. Reich of the United States Geological Survey. Note that the station gauges were washed out due to Hurricane Mitch in 1998. Monthly average rainfall is also plotted for Belize City and Guatemala City, which have the longest ~continuous records in the region, obtained from the World Monthly Surface Station Climatology supplied by the Data Support Section of the Computational and Information Systems Laboratory at the National Center for Atmospheric Research. Note the different scales on each y-axis.

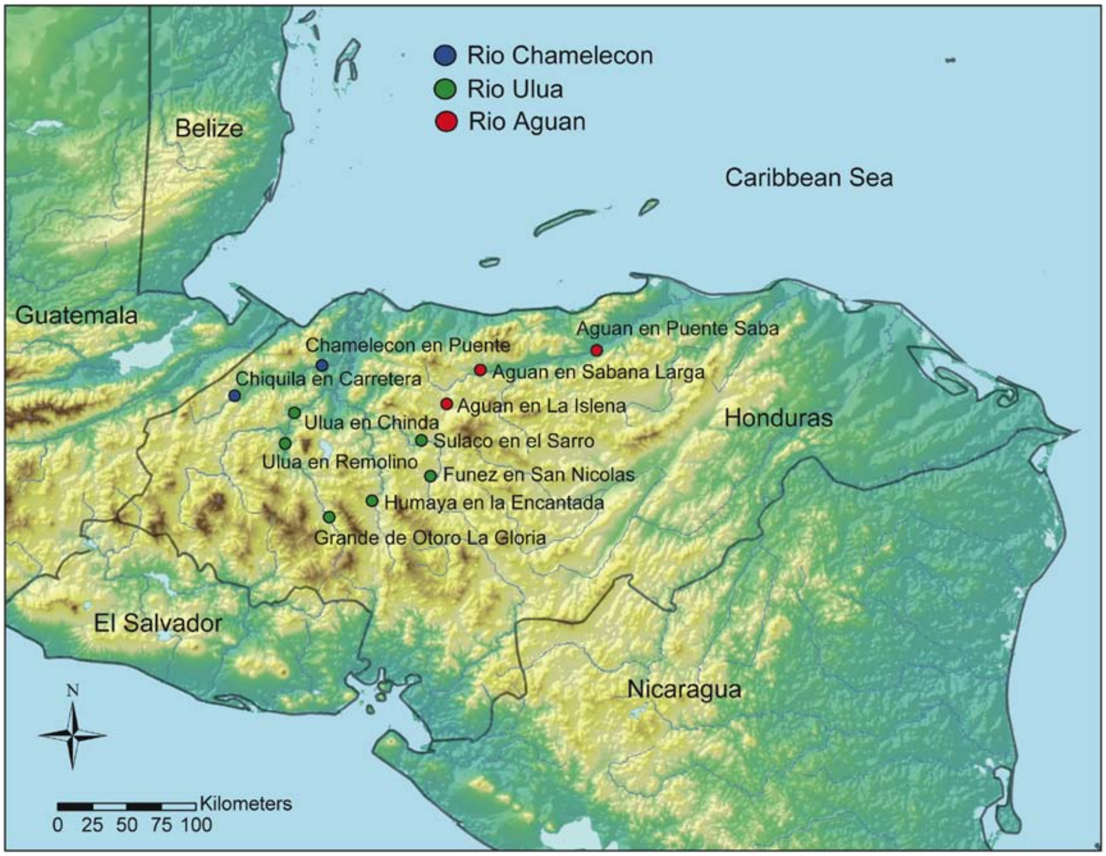

Figure 5-7. Map of locations of river gauging stations for records plotted in Fig. 5-6.

Increasing runoff may be negatively affecting corals at the Sapodilla Cayes, which experiences the highest levels of sedimentation, according to the relative Ba/Ca concentrations. Long-term records compiled from multiple coral colonies from each site show declining growth rates at the Sapodilla Cayes beginning in the 1970's (Carilli et al. in review). In addition, by the time cores were collected in 2006 and 2007, corals at this site had not yet recovered from growth suppression due to a severe bleaching event in 1998 (Carilli et al. in press). These growth effects reflect sublethal chronic stress, probably due to the negative impacts of increasing runoff at this site.

CONCLUSIONS

These century-scale coral geochemical records indicate that as development and agriculture expand in Honduras, Guatemala, and Belize, the adjacent reef system is experiencing higher levels of runoff. In addition, these records confirm that runoff impacts are concentrated near the main input sources in the south. The Sapodilla Cayes and Cayos Cochinos, the two sites that experience the highest runoff impacts, are both marine reserves. However, designation as a marine reserve does not necessarily influence the amount of runoff entering the reserve. Given previous work showing river-reef connectivity in the Meso-American Region (Andréfouët et al. 2002, Chérubin et al. 2008, Paris and Chérubin 2008, Soto et al. 2009) and the deleterious effects on corals from sedimentation and heavy metals (Rogers 1990, Peters et al. 1997), I suggest that efforts should be focused on reducing runoff from the land into these marine protected areas. Examples of measures to reduce the impact of land-based runoff include replanting mangroves to trap sediment and attached pollutants at the coast, maintaining vegetative barriers along waterways to prevent eroded material from entering the drainage system, and terracing steep hillsides to reduce soil erosion.

Although more distal sites like Turneffe and Utila experience lower overall amounts of runoff, the steady increase in land development and associated runoff across the entire reef shows that without changes in land use practices, these reefs will likely become more degraded in the future. Because local impacts such as sedimentation and nutrient loading likely reduce a coral's thermal tolerance, the combination of increasing runoff and water temperatures is likely to be devastating for the future of coral reefs (Knowlton and Jackson 2008, Wooldridge 2009). Therefore, reducing local impacts such as runoff may increase the likelihood of corals surviving into the future.

Table 5-5. Long-term average and standard deviation of each metal/Ca from each site in μmol/mol. Time series are of different lengths for each site; Turneffe: 1892-2005, Utila: 1907-2005, Cayos Cochinos: 1844-2006, Sapodilla 1901-2006.

Site Metal/Ca	Turneffe Average, *σ (±)*	Utila Average, *σ (±)*	Cayos Cochinos Average, *σ (±)*	Sapodilla Average, *σ (±)*
Ba/Ca	3.41,	3.60,	3.68,	3.84,
	0.218	*0.172*	*0.224*	*0.274*
Mn/Ca	1.24,	2.03,	2.85,	2.57,
	0.741	*1.302*	*2.904*	*1.519*
Cr/Ca	0.71,	1.26,	3.02,	2.55,
	0.664	*1.720*	*5.036*	*3.070*
Sb/Ca	1.60E-02,	2.49E-02,	4.01E-02,	5.72E-02,
	9.24E-03	*3.64E-02*	*4.66E-02*	*6.83E-02*
Cu/Ca	0.16,	0.30,	0.47,	0.45,
	0.227	*0.478*	*0.557*	*0.424*
Zn/Ca	2.84,	5.25,	5.19,	6.42,
	16.8	*14.4*	*10.6*	*16.8*
Pb/Ca	0.17,	0.18,	0.21,	0.28,
	0.446	*0.227*	*0.220*	*0.385*

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CHAPTER 6: Multi-decadal coral skeletal records of carbon and oxygen isotopes from the Mesoamerican Reef

ABSTRACT

Fluctuations in stable carbon and oxygen isotopes contained in coral skeletons are related to changes in metabolic processes (carbon) and seawater temperature and salinity (oxygen). These records can therefore be used to reconstruct environmental conditions experienced by the corals while they were growing, and provide useful information in regions or time periods where instrumental data are sparse or unavailable. Here I produced records on the order of 70-90 years long from four sites on the Mesoamerican Reef: Turneffe Atoll, the Sapodilla Cayes, Utila, and Cayos Cochinos. I find significant isotopic variability between sites, but my record from Turneffe Atoll closely replicates that from the same area collected by other researchers. I find variability in both isotopic records in frequency bands generally on the order of 2-4 years, 4-6 years, and a few records contain longer periodicity. The isotope records appear most strongly related to the El Niño-Southern Oscillation.

INTRODUCTION

Scleractinian corals continuously secrete a calcium carbonate skeleton that captures a record of the environment in which it was precipitated (Barnes and Lough 1996). The oxygen isotopic signature of the coral skeleton is related to the isotopic signature of the surrounding seawater (which is related to salinity) and the temperature at which the skeleton is precipitated (Linsley et al. 1999). Both higher temperatures and fresher water result in a lighter (more negative) oxygen isotopic composition. The carbon isotopic signature of the coral skeleton is mostly controlled by the amount of photosynthesis in the symbiotic zooxanthellae (Swart 1983). As photosynthetic rate increases, the zooxanthellae preferentially uptake light carbon, leaving the skeletal signature heavier (more positive). The relative amount of autotrophy versus heterotrophy (Grottoli 2002, Grottoli et al. 2006), the carbon source (Swart et al. 1996), and coral skeletal growth rates can also affect coral skeletal carbon isotopes (McConnaughey 1989).

Stable isotope records from coral skeletal cores have been used in recent decades to reconstruct paleoclimate from tropical regions worldwide, and have been instrumental in investigations of oceanic climate oscillations such as the El Niño Southern Oscillation (eg. Dunbar et al. 1994, Charles et al. 1997, Crowley et al. 1997, Cobb et al. 2003, Hetzinger et al. 2008). Finding locations where corals record certain climatic oscillations of interest is therefore important for paleoclimate reconstructions and future climate forecasts.

Caribbean SST and rainfall are affected by El Niño-Southern Oscillation (ENSO) variability (Enfield and Mayer 1997, Giannini et al. 2000) and the migration of the Intertropical Convergence Zone (ITCZ) (Linsley et al. 1994, Giannini et al. 2000). However, there is also evidence that coral proxy records from the Caribbean can capture variability associated with other climatic oscillations including the Tropical North Atlantic Index (TNAI; described by Penland and Matrosova 1998) (Gischler and Oschmann 2005) and the Atlantic Multidecadal Oscillation (AMO; described by Enfield 2001) (Hetzinger et al. 2008, Saenger et al. in press).

In addition, the isotopic record from one core that Gischler and Oschmann (2005) analyzed from inside the lagoon at Turneffe Atoll was not well correlated with their other records from the Mesoamerican Reef, or with climatic variables. The differences between the Turneffe record and those from the barrier reef were attributed to restricted flow within the lagoon, which may cause fluctuations in salinity and temperature unrelated to larger-scale climatic processes. Here I expand on this study by investigating additional records of both oxygen and carbon stable isotopes from corals collected from four sites on the Mesoamerican Reef to determine which large-scale climatic oscillations these records capture, as well as regional-scale variability in these signals.

MATERIALS AND METHODS

Cores were collected from *Montastraea faveolata*, the dominant reef builder on the deep fore reef in Mesoamerica (McField 2000) from four sites on the Mesoamerican Reef: Turneffe Atoll, the Sapodilla Cayes, Utila, and Cayos Cochinos (Fig. 6-1). Cores were drilled vertically to capture the maximum growth axis using a pneumatic drill with a core barrel of 5 cm diameter. After collection, tissue was removed with a waterpik and cores were rinsed in freshwater and air-dried. Upon return to the Scripps Institution of Oceanography, an 8 mm thick slab was removed from each core using a carbide-tipped double-bladed table saw lubricated with water. X-rays of these slabs were taken at Thornton Hospital to reveal annual density bands (Knutson et al. 1972).

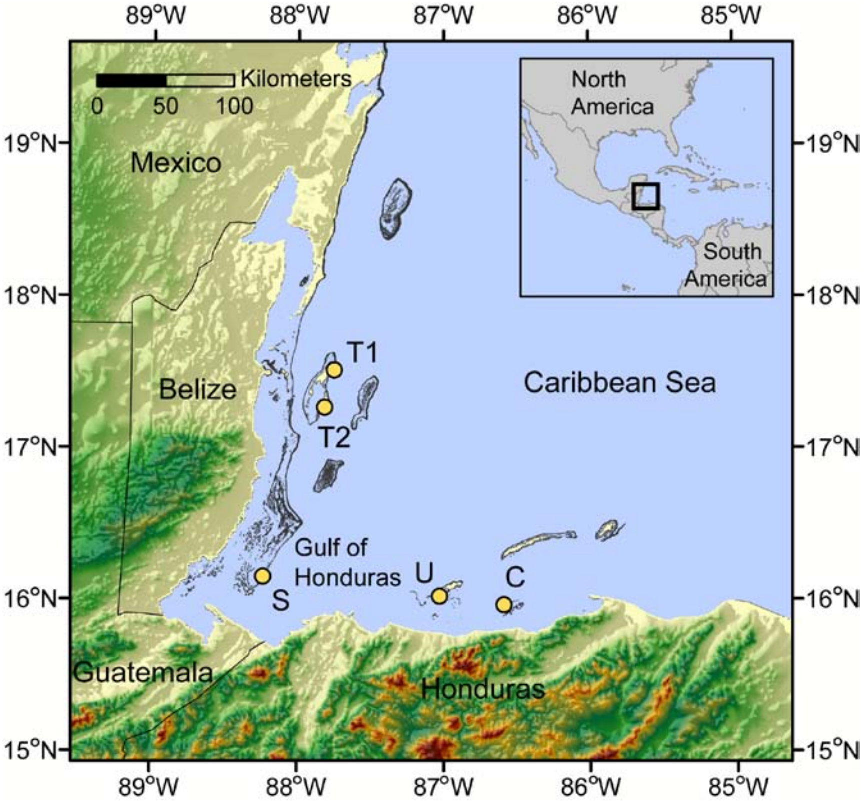


Figure 6-1. Map of the Mesoamerican Reef (dark gray) with coral collection sites (yellow circles) and surrounding region with topography. Note the higher relief in the south, where rainfall and runoff are concentrated.

Samples of ~200-300 μg skeletal powder were drilled along corallite walls using a small drill press and a drill bit ~0.5 mm in diameter. Samples were spaced 1 mm apart along most of all cores, but 0.5 mm apart near tops of cores with compressed growth. Each sample was reacted in a common phosphoric acid bath at 90°C for 11 minutes, then run through a Finnigan MAT 252 stable isotope ratio mass spectrometer. Each set of 40 unknowns included 7 interspersed standards of ground *Porites sp.* coral to quantify instrumental precision. Dates were assigned to each sample by comparison with growth bands from X-rays and expected annual cycles based on SST (Fig. 6-2, 6-3). Isotopic ratios are expressed in permil (‰) notation versus the Pee Dee Belemnite (PDB) standard:

$$\delta^{18}\mathrm{O} = \left[\frac{{}^{18}\mathrm{O}/{}^{16}\mathrm{O}_{\mathrm{sample}} - {}^{18}\mathrm{O}/{}^{16}\mathrm{O}_{\mathrm{standard}}}{{}^{18}\mathrm{O}/{}^{16}\mathrm{O}_{\mathrm{standard}}} \right] * 1000\text{‰}$$

Two years of in situ water temperature and salinity data, collected at 10 minute intervals by a Seabird 16-plus instrument placed at the Cayos Cochinos site by the USGS, were also used to model the predicted monthly oxygen isotopic anomalies that corals would have recorded over this time period, using the scaling 0.15‰ per 1°C + 0.25‰ per 1 psu salinity (Fig. 6-4). Long-term trends in carbon isotopes were estimated by fitting a linear regression to each dataset with respect to time.

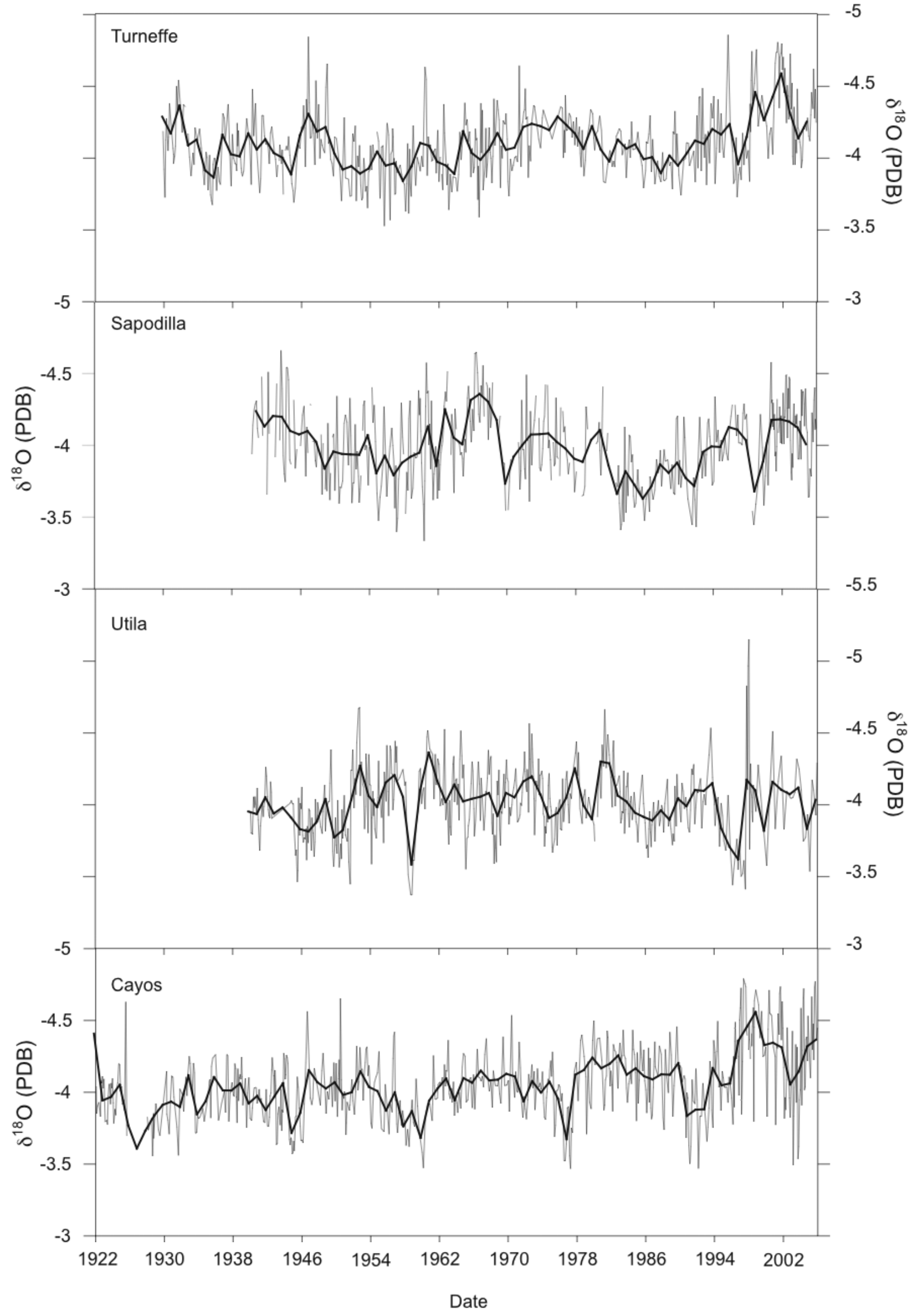


Figure 6-2. Monthly (thin line) and annual average (thick line) ratios of oxygen isotopes expressed as δ^{18}O (versus PDB) at all four sites. Note that the y-axis is reversed so that more negative values, corresponding to warmer and wetter conditions, is up.

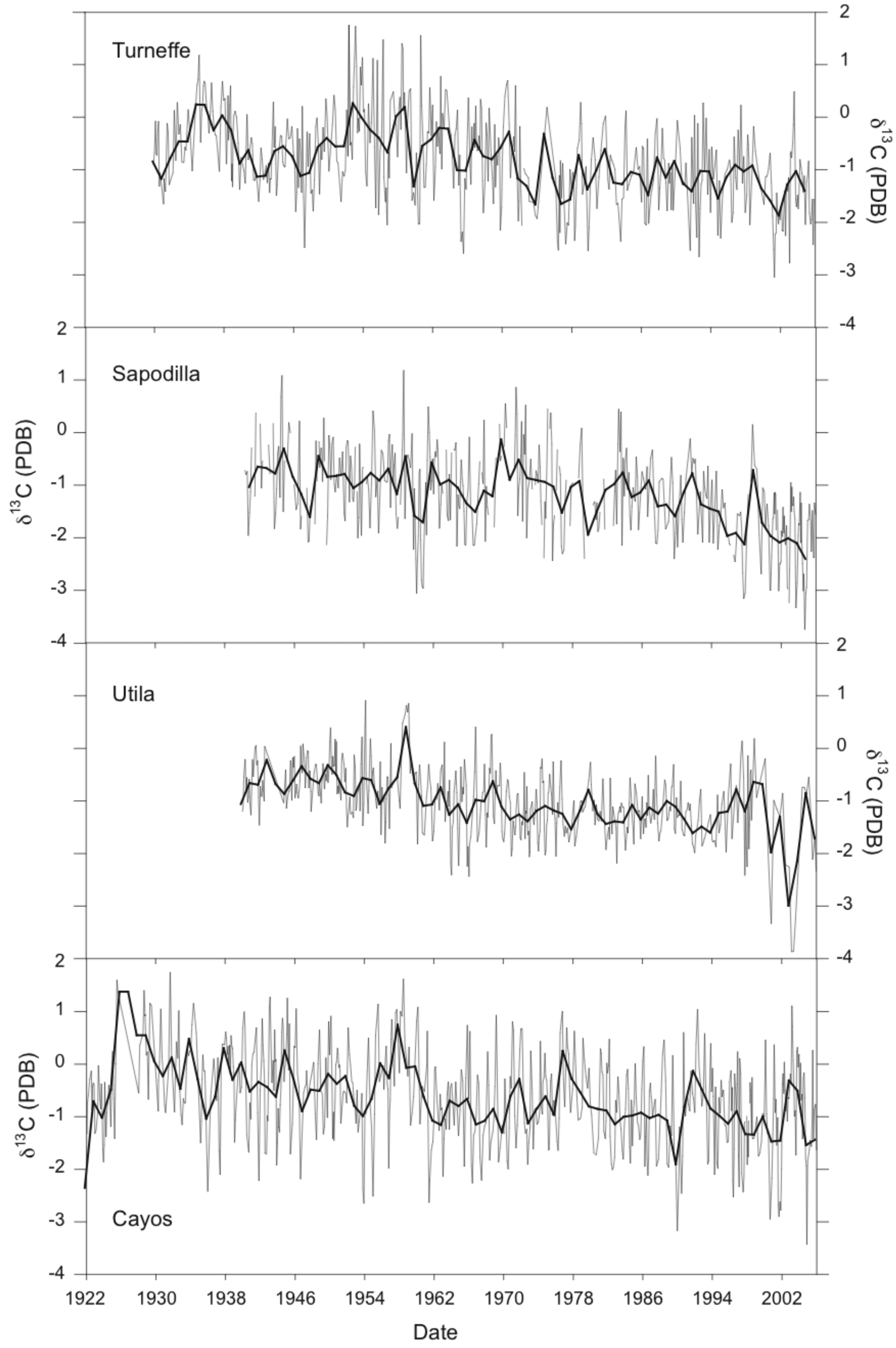


Figure 6-3. **Monthly (thin line) and annual average (thick line) ratios of carbon isotopes expressed as δ^{13}C (versus PDB) at all four sites.**

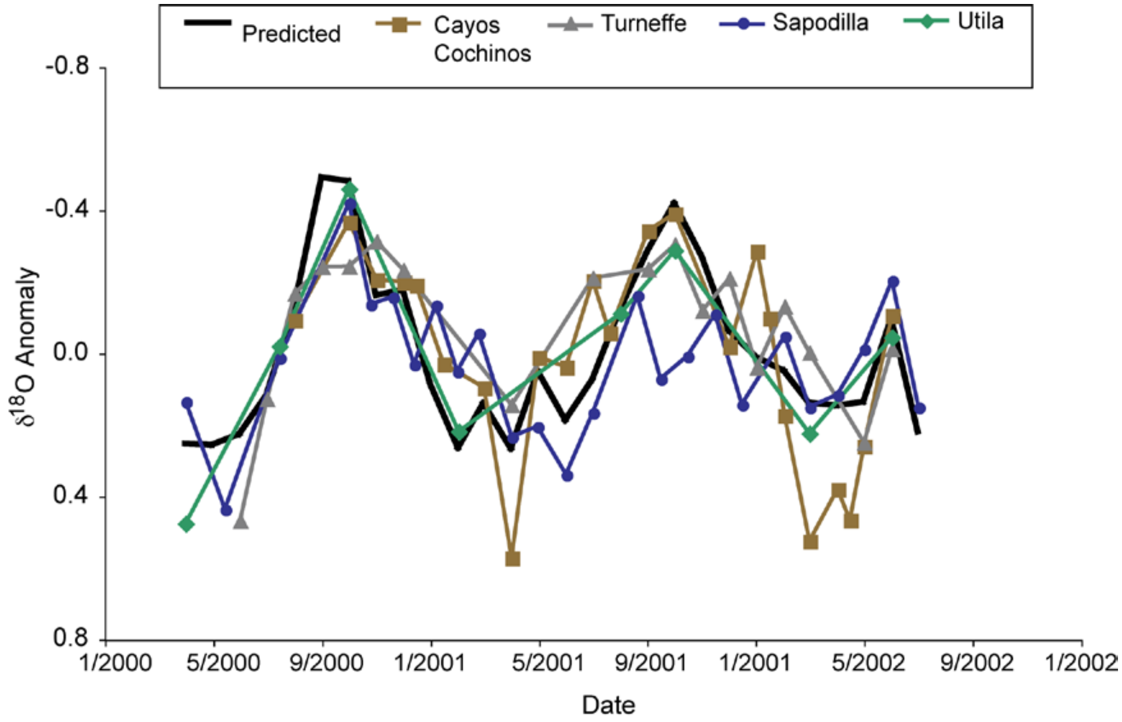


Figure 6-4. Predicted monthly oxygen isotopic anomalies from in situ temperature and salinity data collected from the Cayos Cochinos site, with measured isotopic anomalies at all sites.

I investigated relationships between the isotopic records, sea surface temperature, and various climatic indices using several techniques. First, I investigated periodicity in the frequency domain by plotting the spectra of selected climatic indices using Welch's periodograms in Matlab (not shown). Periodogram specifications were the following: each dataset had segment lengths of 128 datapoints; these were overlapped by 50%, NFFT was set to 265, and the sampling frequency was 12 (for monthly climatic data). The climatic indices that I investigated were the Atlantic Meridional Oscillation (AMO; Enfield et al. 2001), North Atlantic Oscillation (NAO; Hurrel 1995), Tropical North Atlantic Index (TNAI, Penland and Matrosova

1998), Caribbean Index (CAR; Penland and Matrosova 1998), Pacific Decadal Oscillation (PDO; Schwing et al. 2002), and the Multivariate El Niño Southern Oscillation Index (MEI; Wolter and Timlin 1998).

Next, I investigated the periodicity of fluctuations in my isotope data in the frequency domain, to determine if the isotopic records contained oscillations that matched the frequencies of the climatic variables investigated above. First, I interpolated the data to an evenly spaced timescale using the average number of samples/year as in the original data (7 for Sapodilla and Turneffe, 8 for Cayos Cochinos and Utila) with a spline interpolation in Matlab. These interpolated data were then linearly detrended and the mean was removed before the spectral density was estimated as above, except that the sampling frequency was set to 7 for Sapodilla and Turneffe and 8 for Cayos Cochinos and Utila (Figs. 6-5, 6-6).

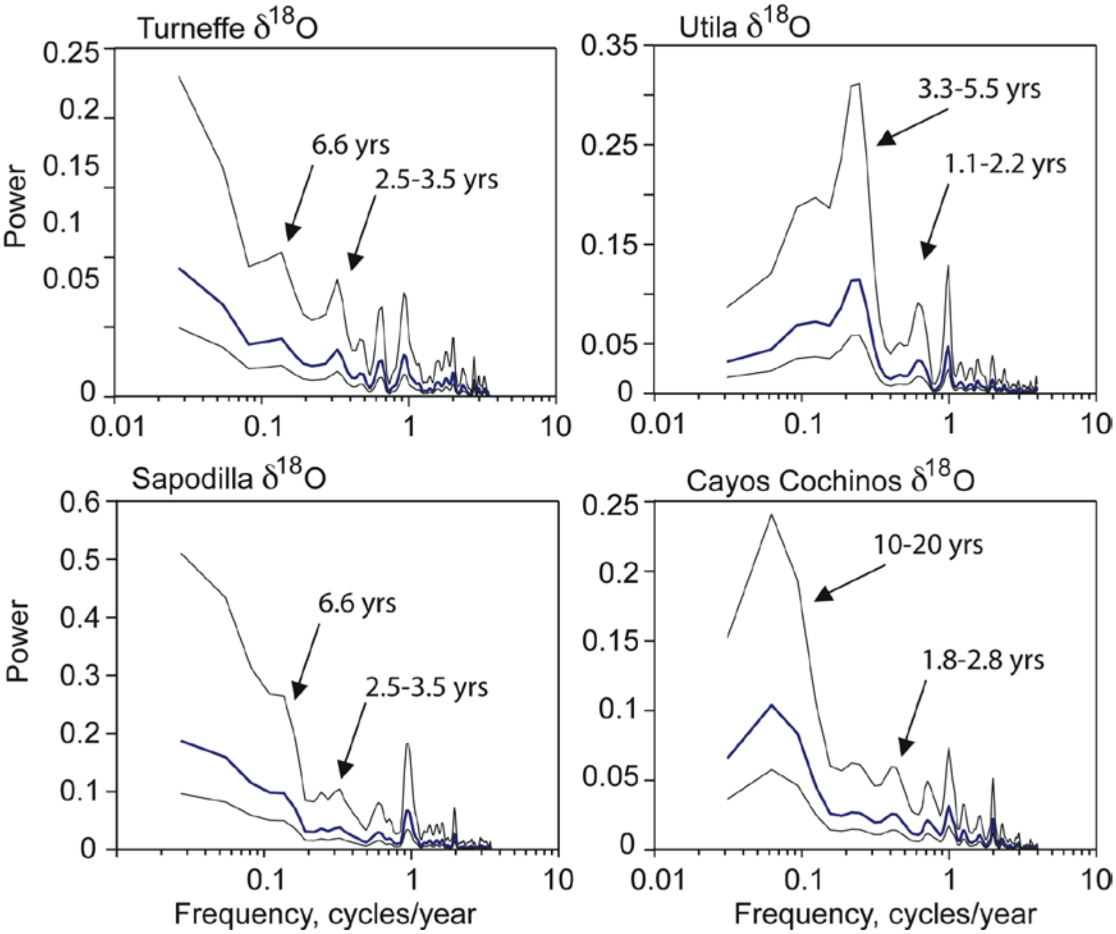


Figure 6-5. Spectra of oxygen isotope records (blue) with 95% confidence intervals (black) and approximate peak periods longer than one year.

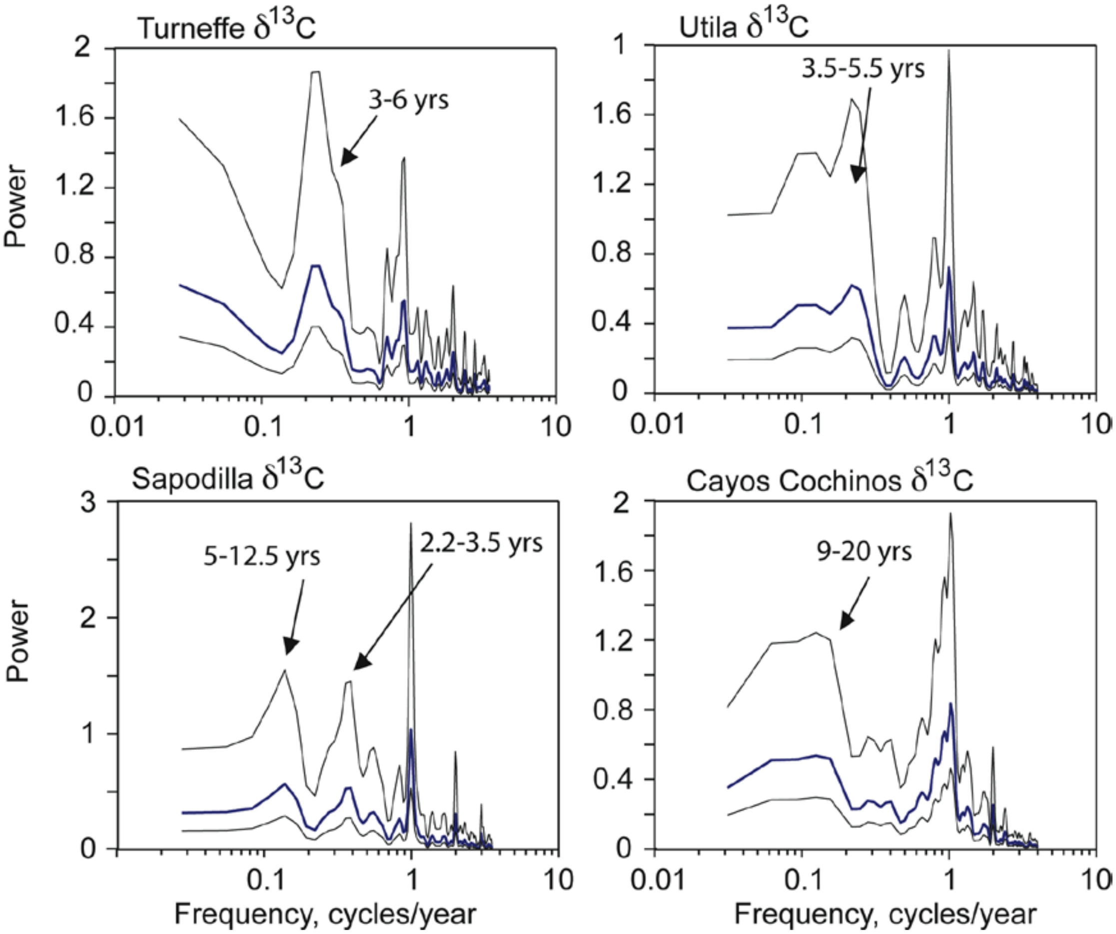


Figure 6-6. Spectra of carbon isotope records (blue) with 95% confidence intervals (black) and approximate peak periods longer than one year.

I then investigated how variability in the isotope records was related to global SST and outgoing longwave radiation (OLR) anomalies using monthly SST anomaly data from the Kaplan Extended v2 dataset (Kaplan et al. 1998) and monthly OLR data from the NOAA NCEP CPC Global dataset. The purpose of this investigation was to determine whether global patterns in SST and OLR anomalies that are associated with a specific climatic oscillation (for instance ENSO or the PDO) would be evident in the isotopic variability. I first interpolated the isotope data to monthly resolution using a spline interpolation, then detrended and demeaned the records. I next used a zero-pole-gain bandpass filter in Matlab to remove all periodicity except for that within a specified range around the main spectral peak for each individual isotope record (Fig. 6-5, 6-6). The investigated bandwidths were: for Turneffe, 2-4 years and 3-6 years for oxygen and carbon isotopes, respectively; for Sapodilla, 2-4 years for oxygen isotopes, and both 2-4 years and 5-13 years for carbon isotopes; for Utila, 3-6 years for both oxygen and carbon isotopes; and for Cayos Cochinos, 1.8-3 years and 2-4 years for oxygen and carbon isotopes, respectively. I then picked out the months during which the filtered isotope records were either in the positive extreme phase or the negative extreme phase, using a cutoff that differed between records and was based on the relative range of oscillations in each, a created a vector of dates for both the extreme positive and negative filtered isotopic records at each site. I then averaged the global SST anomaly and OLR maps for the dates contained in each positive and negative extreme vector, respectively, creating one average SST and OLR global map corresponding to the dates in which the isotopic records were in either extreme. These averaged SST anomaly and OLR maps were then differenced to create the plots shown in figures 6-7 and 6-8, which show the difference in SST and OLR anomalies, respectively, during different extreme phases recorded in the isotope records in a certain bandwidth.

Figure 6-7 (facing page). Global maps of differences in SST anomalies between time periods with positive and negative extremes in each filtered isotopic record, denoted above each map. White numbers in lower left corner are anomalies from the grid cell associated with the Mesoamerican Reef.

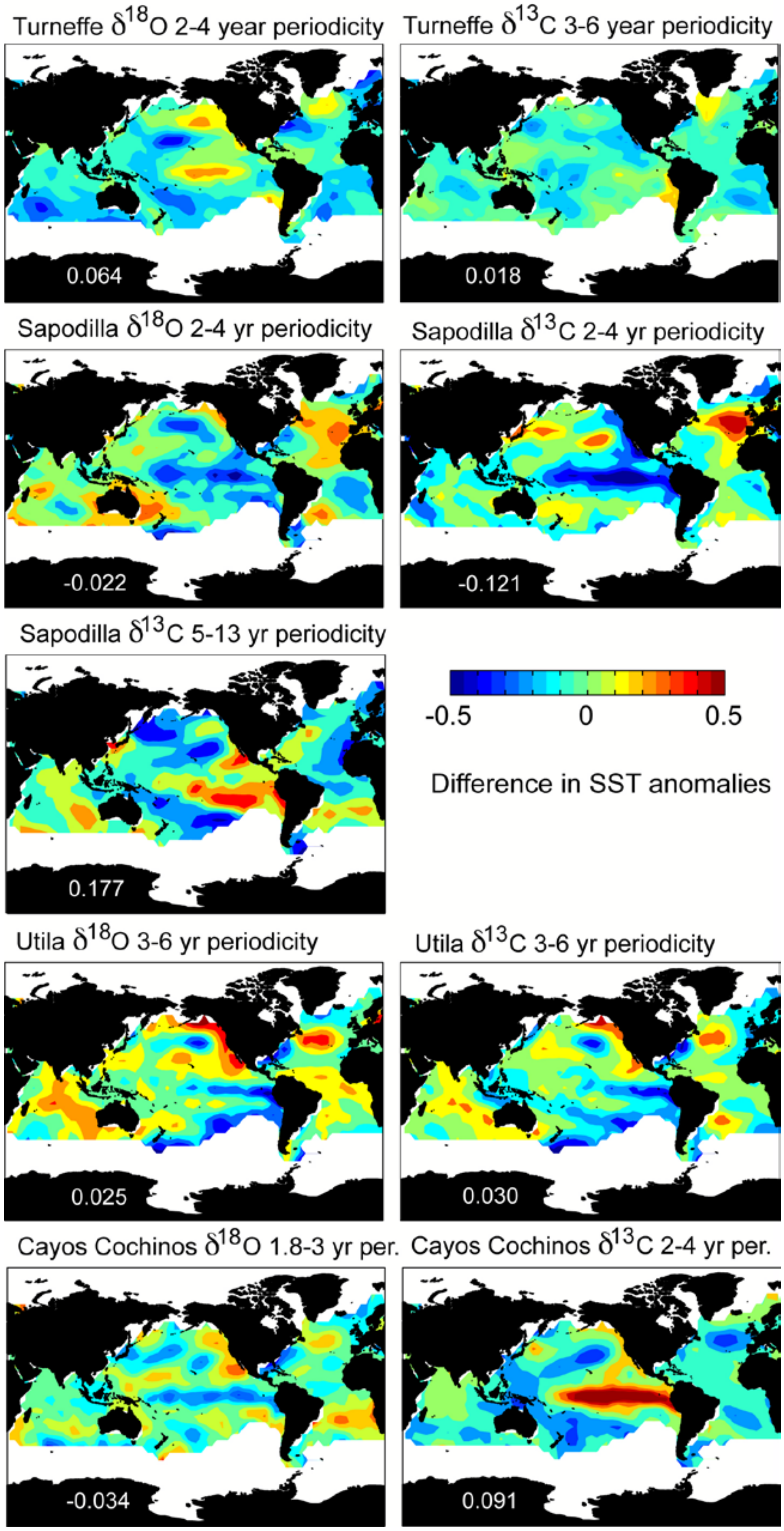
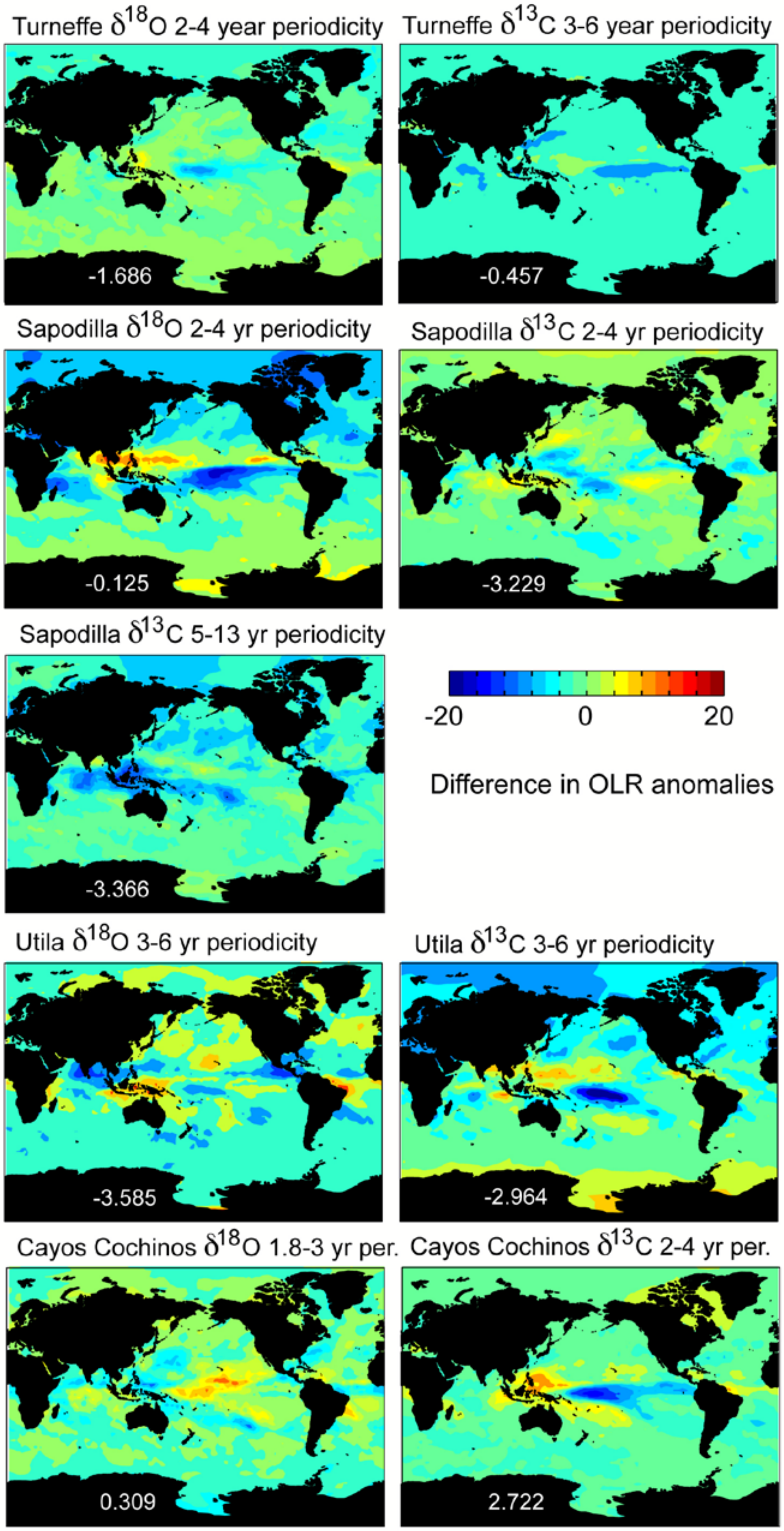

Turneffe δ18O 2-4 year periodicity
0.064
Turneffe δ13C 3-6 year periodicity
0.018
Sapodilla δ18O 2-4 yr periodicity
-0.022
Sapodilla δ13C 2-4 yr periodicity
-0.121
Sapodilla δ13C 5-13 yr periodicity
0.177
-0.5
0
0.5
Difference in SST anomalies
Utila δ18O 3-6 yr periodicity
0.025
Utila δ13C 3-6 yr periodicity
0.030
Cayos Cochinos δ18O 1.8-3 yr per.
-0.034
Cayos Cochinos δ13C 2-4 yr per.
0.091

Figure 6-8 (facing page). Global maps of differences in OLR anomalies between time periods with positive and negative extremes in each filtered isotopic record, denoted above each map. White numbers in lower left corner are differences in OLR from the grid cell associated with the Mesoamerican Reef.


Turneffe δ^{18}O 2-4 year periodicity
-1.686
Turneffe δ^{13}C 3-6 year periodicity
-0.457
Sapodilla δ^{18}O 2-4 yr periodicity
-0.125
Sapodilla δ^{13}C 2-4 yr periodicity
-3.229
Sapodilla δ^{13}C 5-13 yr periodicity
-3.366
-20
0
20
Difference in OLR anomalies
Utila δ^{18}O 3-6 yr periodicity
-3.585
Utila δ^{13}C 3-6 yr periodicity
-2.964
Cayos Cochinos δ^{18}O 1.8-3 yr per.
0.309
Cayos Cochinos δ^{13}C 2-4 yr per.
2.722

RESULTS

Oxygen isotope records from all four sites follow the pattern predicted by scaling monthly-averaged in-situ temperature and salinity fluctuations fairly well (Fig. 6-4). Differences between the predicted and measured pattern may stem from differences in the effects of freshwater runoff or evaporation at each site. Freshwater runoff is typically depleted in the heavy oxygen isotope, and increases in freshwater runoff (decreased salinity) lead to seawater with a lighter $\delta^{18}O$ signature. Conversely, during evaporation (increased salinity), the lighter oxygen isotope is preferentially removed, leaving seawater with a heavier $\delta^{18}O$ signature. Other differences may stem from sampling different parts of the corallite in addition to the skeletal wall.

All sites have similar long-term trends in carbon isotopes, decreasing by 0.13‰ per decade at Turneffe and Cayos Cochinos, 0.15‰ per decade at Utila, and 0.16‰ per decade at Sapodilla. At all sites, oxygen and carbon isotopes are positively correlated with one another within cores: correlations range from R=0.45 at Utila to 0.61 at Cayos Cochinos.

Spectral analyses (Figs. 6-5, 6-6) indicate that in general, there is variability with a 2-4 year and 4-6 year periodicity. Peaks were identified in the records as follows: 2.5-3.5 year and 6.6 year periodicity in the Turneffe oxygen isotope record, and 3-6 year periodicity in the Turneffe carbon isotope record; 2.5-3.5 year and 6.6 year periodicity in the Sapodilla oxygen isotope record, and 2.2-3.5 year and 5-12.5 year periodicity in the Sapodilla carbon record; 1.1-2.2 year and 3.3-5.5 year periodicity in the Utila oxygen isotope record, and 3.5-5.5 year periodicity in the Utila carbon isotope record; 1.8-2.8 year and 10-20 year periodicity in the Cayos Cochinos oxygen isotope record and 2-4 year and 9-20 year periodicity in the Cayos Cochinos carbon isotope record.

Most of the mapped differences in SST anomalies and OLR have patterns that appear to be related to the El Niño-Southern Oscillation (Fig. 6-7, 6-8). These patterns consist of strong differences in SST anomalies and OLR near the equator in the Pacific, and with different signs in the eastern versus the western Pacific. For instance, the mapped differences in SST anomalies and OLR constructed using the Cayos Cochinos carbon isotope record's extremes, which was filtered at a period of 2-4 years show warming in the eastern Pacific and cooling in the western Pacific, and lower OLR (higher clouds) in the eastern Pacific and higher OLR in the western Pacific, respectively. Both of these patterns are consistent with the patterns seen during an El Niño event, with relatively warmer waters and higher clouds in the eastern Pacific and lower water temperatures and cloudiness in the western Pacific.

DISCUSSION

Although there are differences in the oxygen isotopic records between sites, the apparent similarity of the Turneffe records between this study and Gischler and Oschmann (2005) indicates that records from a single site may be reproducible (Pearson correlation coefficient on annual averages $R^2 = 0.34$, Fig. 6-9). However, there are larger differences on a regional (10's of km) scale apparent in the records presented here, which may be caused by actual differences in environmental variability between sites, but may also be affected by differences in the confounding influence of salinity change on the SST signal (oxygen isotopes) or differences in source-water or heterotrophy signals (carbon isotopes).

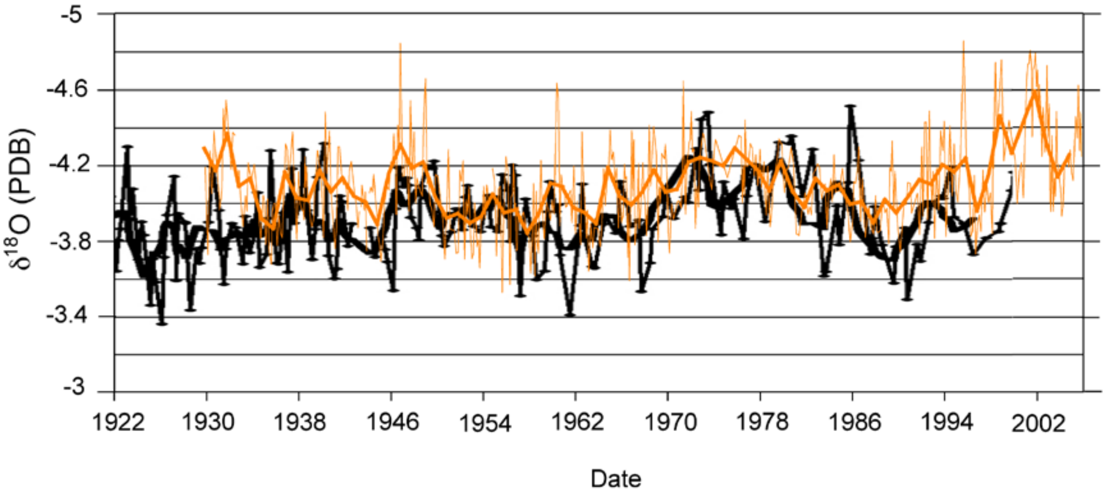


Figure 6-9. Comparison of oxygen isotopic records from Turneffe Atoll. Black: lagoonal core record reproduced from Gischler and Oschmann (2005); Orange: Turneffe record from this study. Thick lines are annual averages (R^2 = 0.34).

Oxygen isotopes from all sites investigated here are likely to be affected significantly by changes in salinity through different processes at each site. The more northerly site, Turneffe, is the least influenced by land-based runoff (Chérubin et al. 2008, Prouty et al. 2008, Carilli et al. in review), as most of the rainfall and freshwater discharge is concentrated in the south (Thattai et al. 2003). However, the Turneffe lagoon may affect the local salinity via evaporative processes due to restricted flow (Gischler and Oschmann 2005). Indeed, although my core from Turneffe Atoll was collected outside the lagoon, it was located approximately 0.5 km from a channel into the lagoon, and therefore lagoonal waters may have influenced the isotopic signature, as suggested by the similar pattern between my oxygen isotopic record and that of Gischler and Oschmann (2005) whose core was collected inside the lagoon (Fig. 6-9). Therefore, between-site differences in salinity due to evaporation and/or runoff may be responsible for observed differences in δ^{18}O between sites. Likewise, differences in δ^{13}C between sites may be related to differences in the dissolved inorganic carbon δ^{13}C in the surrounding seawater (Swart et al. 1996), zooxanthellae photosynthesis (Swart 1983), the relative amounts of auto- versus heterotrophy (Grottoli 2002), and/or coral calcification rates (McConnaughey 1989). Because of these potential artifacts that could be responsible for observed differences in isotopic records between sites, though costs increase substantially, it is likely preferable to utilize multiple records from each site or from a region to reconstruct climate (Linsley et al. 1999, Watanabe et al. 2002), or to use additional proxies, for instance using Sr/Ca to untangle the relative effects of SST and salinity change on δ^{18}O (Beck et al. 1992).

Spectral analysis and the investigation of differences in SST and OLR between positive and negative phases of significant periodicity in the isotope records indicate that the coral skeletal isotopic composition of this region is probably mostly influenced by ENSO (here represented by the MEI). The other climatic indices investigated here may also have competing or additive influences. This may explain why during some time periods the isotopic records appear similar to the MEI (for instance from 1950-1975 the annual average Turneffe carbon isotope record appears very similar to the MEI), while during others they do not (after 1975 the Turneffe carbon isotope record and the MEI appear less closely related) (Fig. 6-10, 6-11).

The long-term trends in decreasing carbon isotopic signature may reflect the influence of the Seuss effect, whereby burning fossil fuels releases lighter (more negative) carbon into the atmosphere, which then mixes through the carbon cycle (Keeling 1979). Indeed, the trends observed here, decreasing 0.13-0.16‰ per decade is consistent with that seen in ocean surface waters with a global average change estimated variously at ~0.15‰ per decade (Sonnerup et al. 1999) and ~0.18‰ per decade (Gruber et al. 1999).

In conclusion, the variability between records from different parts of the Mesoamerican Reef presented here indicates that future paleoclimate work in this region should interpret records from a single coral core with caution. The combination of isotopic measurements with coupled Sr/Ca measurements (which are not affected by salinity, but only temperature) may be useful for separating these influences, and may provide a more robust paleoclimate proxy than stable isotopes in this region.

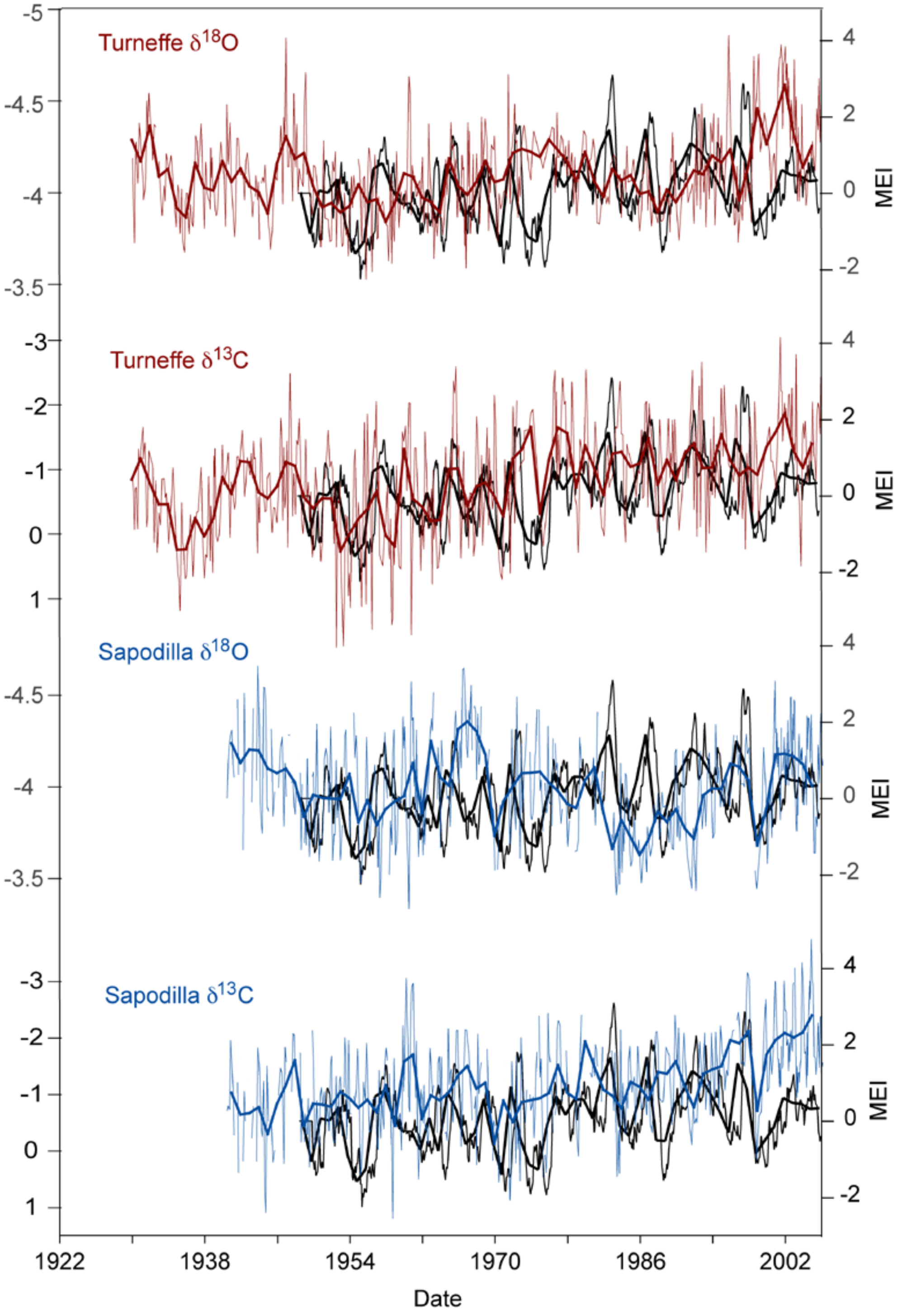


Figure 6-10. Comparison of isotopic records from Turneffe and Sapodilla with the MEI index. Thick lines are annual averages.

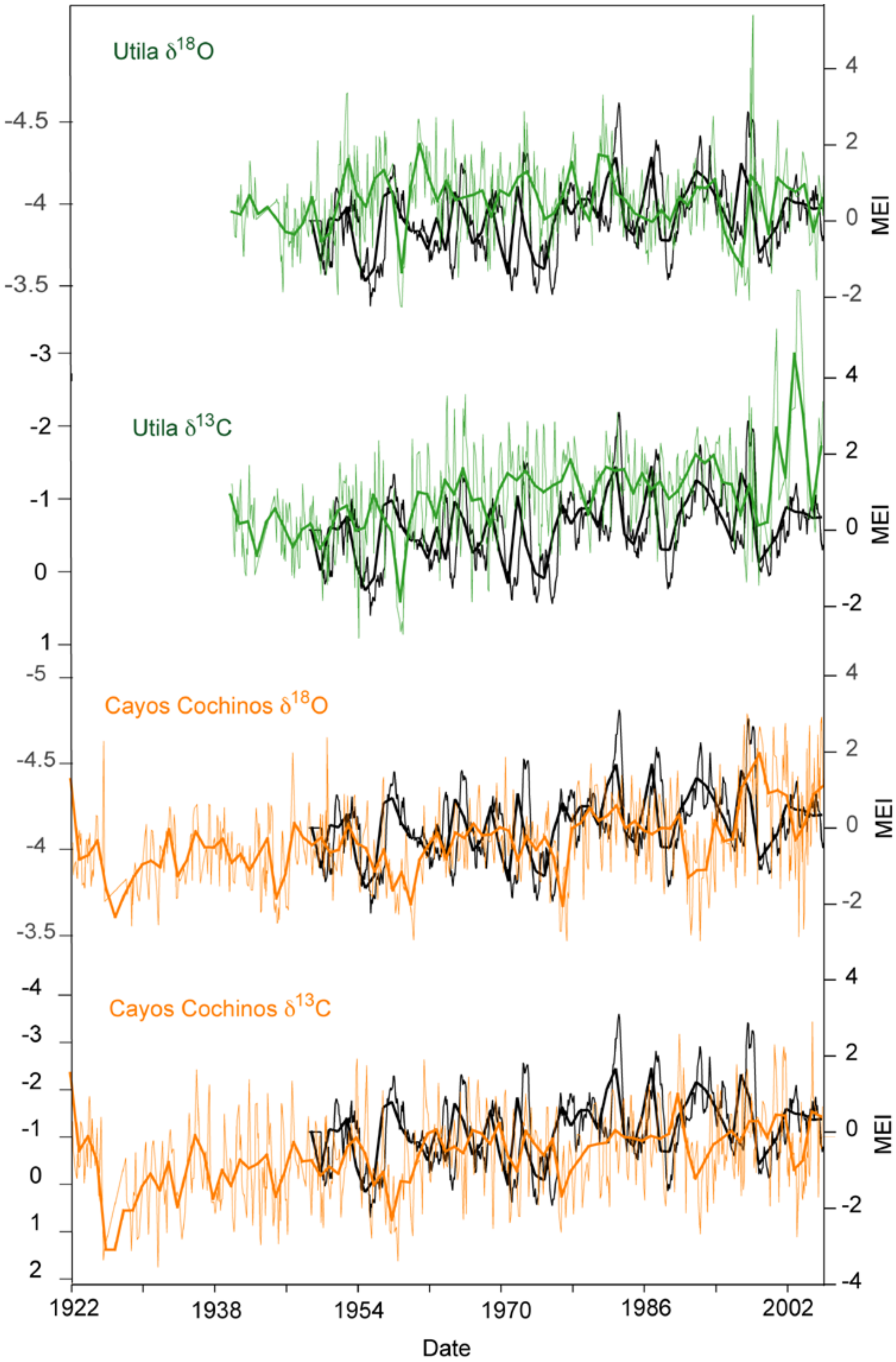


Figure 6-11. Comparison of isotopic records from Utila and Cayos Cochinos with the MEI index. Thick lines are annual averages.

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CHAPTER 7: Summary of the Dissertation

SUMMARY OF THE DISSERTATION

This dissertation investigated the recent history of coral growth rates and environmental change on the Mesoamerican Reef. I found significant differences in coral resistance to and recovery after the 1998 mass coral bleaching event between sites, and found that resistance and resilience to bleaching were both higher at sites with lower background anthropogenic stress. I also found that the 1998 bleaching event was unprecedented over the past century, despite the fact that temperatures mid-century were equally warm. This suggests that the reason for widespread bleaching on the Mesoamerican Reef in 1998 was a reduction in coral thermal tolerance owing to local background stress. Supporting the idea that stress has increased towards the present, I found significant increases over time in the occurrence of bands of high concentrations of endolithic algae; I hypothesize that these bands are remnant records of blooms that occurred during periods of coral paling. My geochemical records from one long core from each site show that sediment-laden runoff has increased at all sites over the past century, but the pattern of differences between sites has remained constant. These data are consistent with the idea that human-induced stressors have steadily increased, and also suggesting that differences in background stress between sites have been consistent through time. My isotopic records show that there is significant variability in environmental conditions between the four sites: they are not all consistently recording the same climatic signals. However, they all appear to contain periodicity consistent with forcing from the El Niño-Southern Oscillation.

This dissertation made novel use of tree-ring statistical techniques and large sample sizes to construct robust measures of coral growth rate and the frequency of endolithic algal blooms. I found that at least 6-9 cores per reef are necessary to construct a robust measure of coral growth rates; a large sample size is also important for investigations of endolith bloom frequency, especially because some blooms are discontinuous across cores.

CONSERVATION IMPLICATIONS

This research indicates that runoff from the mainland is likely having a significant effect on coral health in Mesoamerica, by reducing coral's ability to resist and recover from bleaching. Runoff has the highest impact at the Sapodilla Cayes, but as runoff continues to increase, the other sites may become more severely impacted as well. For this reason I suggest that watershed management, including the implementation of vegetative barriers along waterways, slope terracing, the use of cover crops, and mangrove protection and replanting is an important conservation focus in this region. In addition, other forms of reef protection continue to be important, especially including the effective establishment and maintenance of marine protected areas.

FUTURE WORK

The Mesoamerican Reef is an important natural resource that was once thought to contain some of the healthiest reefs in the Caribbean. I hope that with proper protection, the reef may resume its prior health, and hopefully persist into the future despite a warming climate. Because corals from Sapodilla and Utila showed that they had not yet recovered from the 1998 bleaching event, it would be interesting to return and collect additional cores at a later date to investigate recovery. Because this growth rate suppression was the longest yet recorded, it is hard to predict how much longer the corals will retain this suppressed growth, and this would be an important metric against which to compare future work. In addition, tracking coral recovery from drill-hole scars could be important both in terms of a comparison between sites as well as lending important information for future coring work: how long can we expect it to take before a drill-hole is sealed by new coral growth? Many researchers have collected coral cores but I have yet to see a study as to the lasting effects of these injuries.

A topic that I wasn’t able to explore during this dissertation is how a coral’s background thermal acclimatization may make it more or less able to withstand and recover from bleaching. One way to address this question would be to compare the frequency of stress banding and rate of growth recovery from sites that experience a different range of temperature fluctuations: for instance the Snake Cayes near Punta Gorda, Belize, are in a more restricted-flow environment, so experience a larger range of temperatures than those at the Sapodilla Cayes on the shelf edge (Castillo and Helmuth 2005). It would be interesting to collect cores from the Snake Cayes to compare how thermal acclimatization affects recovery after and resistance to bleaching in this region.

The endolithic algae blooms are still not well understood, though I have determined that they are indeed blooms and not simply accumulated during periods of low coral growth. I attempted to cause artificial blooms in nubbins collected from *M. faveolata* but insufficient aquaria hampered the effectiveness of these experiments. I would like to carry out this work in a more controlled environment, utilizing alizarin red skeletal staining, and isotopic labeling techniques to investigate how coral paling and the addition of nutrients both affect endolith blooms. In addition, further exploration into the patchy nature of endolith blooms could be enhanced by inspecting specimens of slabs of whole coral heads.

Other future research directions include application of the same techniques used here in other environments, for instance in the Line Islands which experience a gradient of human impacts from essentially none (except global change) to significant levels of local fishing. Hawaii is a location that could benefit from these types of hindcast investigations: some reefs there have suddenly collapsed, and investigations of the growth rates may lend some clues as to the cause. Another location where I would like to collect cores for growth rate studies is at St. Croix in the eastern Caribbean. This region has experienced a significantly different thermal history, but also has extensive in situ instrumentation measuring temperature, turbidity, etc. for several years, which would be useful to compare growth rates against. On a similar vein, the installation of intensive in situ instrumentation to characterize temperature, turbidity, nutrient levels, and solar irradiance, coupled with reef surveys including the abundance of fish, algae, and coral health status might be able to establish thresholds at which bleaching is expected, not taking only temperature into account.

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