Trends in Linear Extension Rates for over 100-Year Period in Three Coral Species from Dry Tortugas, Florida

by

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of the requirements for the degree of
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DEDICATION

I dedicate this work to my parents, Hajro and Temima, and to my sister Tea for their selfless support, encouragement, and consideration throughout my academic career.

ACKNOWLEDGMENTS

My work with corals started as a USF internship that Dr. Smoak helped me find. I worked on it at U.S. Geological Survey under the supervision of Dr. Kristine DeLong and directed by Dr. Smoak. Kristine taught me about coral growth patterns and methods of measuring coral extension rates and was always there to answer all of my questions. Without her instructions this work would have been impossible. Soon after I graduated with my B.S., I pursued graduate studies at USF and Dr. Richard Poore offered me to work on my thesis at USGS. I can never express my full gratitude to Dr. Richard Poore for giving me the opportunity to work with some of the greatest scientists in the field. Without Dr. Poore's help and the USGS equipment, x-rays, and software this work would have been impossible to accomplish. I thank Jennifer Flannery, Chris Reich, Ilsa Kuffner, and Don Hickey for their insights, comments, advices, and encouragement throughout my endeavor. I thank my co-advisor Dr. Joseph M. Smoak and the committee member Dr. Kathleen Carvalho-Knighton for their comments, critics, and insights. I am grateful to my friend Tom Harmon for being there to encourage me and give me advice that motivated me in my work. Lastly, I thank my family and friends for their support and encouragement.

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ABSTRACT

Study on 3 coral species, *Montastraea faveolata, Diploria strigosa*, and *Siderastrea siderea* was done to determine the trends in coral linear extension and the impact of sea-surface temperature (SST) and other environmental parameters on a shallow reef system from Dry Tortugas National Park. The extension rates were species-specific. *Montastraea faveolata* had the highest average linear extension and variability (0.84±0.14 (n=165)), followed by *D. strigosa* (0.73±0.06 (n=54)) and *S. siderea* (0.42±0.06 (n=183)) respectively. Two cores of *M. faveolata* had significant correlation with each other (r=0.34, df=67, P=0.0043) and similar long-term patterns although one of them had a higher average linear extension than other. There was no significant correlation between the two *D. strigosa* cores (r=-0.10, df=33, P=0.5676); one of them was affected by hyperplasia tumor. *Siderastrea siderea* PS-A1 core had an overall increasing trend (r=0.64, df=117, P<0.0001) in the extension rates and *M. faveolata* PS-B3 had a decreasing trend (r=-0.22, df=117, P=0.0162). None of the other three cores showed any clear overall trend in the extension rates. *Siderastrea siderea* PS-A1 was correlated significantly with annual SST (r=0.43, df=115, P<0.0001) and warmest month SST (r=0.56, df=115, P<0.0001). Since correlations between the extension rates and SST were positive it suggests that the increase in SST had no negative effect on this species. *Siderastrea siderea* PS-A1 (r=0.73, df=87, P<0.0001) and *M. faveolata* PS-C2 (r=0.32, df=64, P=0.0091) had significant correlations with the sea-level anomaly. *Siderastrea siderea* PS-A1 correlated significantly (r=0.43, df=56, P=0.0008) with Multivariate El

Nino Southern Oscillation Index. There was no significant correlation of Atlantic Multidecadal Oscillation anomaly with any of the cores.

INTRODUCTION

In the past decade there has been some concern over the viability of coral reefs in Florida due to the threats from anthropogenic and natural causes. Significant declines in coral reef cover were reported worldwide (Gardner et al., 2003). The factors cited to affect corals negatively include pollution (Pastorok and Bilyard, 1985; Bjork et al., 1995), nutrient runoff (Tomascik and Sander, 1985; Kuntz et al., 2005), high rate of sedimentation (Rogers, 1990; Humphrey et al., 2008), coral mining (Brown and Dunne, 1988; Shepherd et al., 1992), diseases (Bell, 1992; Hoegh-Guldberg, 1999), coral bleaching (Brown 1997; Rowan et al., 1997; Fitt et al., 2000), decrease in ocean pH (Gattuso et al., 1998; Reynaud et al., 2003), sea level rise (Hubbard et al., 2008; Ogston and Field, 2010), decrease in salinity (Muthiga and Szmant, 1987), increase in water motion (Jokiel, 1978; Dollar, 1982), and changes in sea-surface temperature (SST; Shinn et al., 1966; Carricart-Ganivet et al., 2000).

Coral skeletons made of aragonite precipitated on previously formed skeleton create the distinctive high and low density bands visible on coral x-rays (Highsmith, 1979). These bands proved to be a useful tool in studying coral growth patterns. A couplet of high and low density bands represents approximately one year interval of growth (Hudson et al., 1976). The earliest study on coral growth has been done by Shinn et al. (1966) on *Acropora palmata* using an experimental approach. Since then, several studies were done using the x-ray technology to determine density, extension rate, and calcification of coral skeleton (Buddemeier et al., 1974; Hudson et al., 1976; Dodge and Lang, 1983; Helmle et al., 2011).

One of the parameters of coral growth is the linear extension where the length of an annual band is measured linearly (Hudson et al., 1976; Gladfelter et al., 1978; Carricart-Ganivet et al, 2000). Number of environmental factors was compared to coral extension rates to identify the ones that affected the coral growth and if the coral growth could be used as a proxy for past climates in the tropics (Barnes and Lough, 1996). These studies produced various and often conflicting results. Those that included multiple species found that the extension rates were species-specific and determined by coral genetics (Buddemeier et al., 1974; Tomascik, 1990; Logan et al., 1994). Buddemeier et al. (1974) measured the extension rates of 47 reef-building corals of 15 different species and found that the coral extension rates were determined by a species they belonged to more than by any environmental parameter. Environmental factors known to influence the extension rates include rainfall (Buddemeier et al., 1974; Alibert and McCulloch, 1997), El Nino Southern Oscillation (ENSO) cycle (Alibert and McCulloch, 1997), light levels (Bak et al., 2009), and location within the reef (Cruz-Pinon et al., 2003). Amidst the climate change there is an increasing interest in studying the coral extension rates in relation to ocean pH (Cooper et al, 2008; Gledhill et al., 2008) and SST (Shinn et al., 1966; Carricart-Ganivet et al., 2000).

Multiple studies suggest that the SST is a driving cause of extension rate variability in corals (Shinn et al., 1966; Carricart-Ganivet, 2004; De'ath et al., 2009). Reef building corals need warm water to survive. Their reefs are dominant communities in areas with the SST range between 18 and 30 °C (Hoegh-Guldberg, 1999). In areas beyond this range numbers of coral species decrease and coral reefs are replaced by other communities. Corals require high thermal stability for their survival. Evidence suggests that the average annual SST of tropical oceans fluctuated by less than 2°C in the past 18,000 years. Consequently, high seasonal variations in SST limit coral distribution (D'Croz and Robertson, 1997). Sensitivity to SST, coupled with coral longevity and dead skeleton that can stay intact for several millennia makes corals potentially ideal recorders of the past climate conditions (Barnes and Lough, 1996).

The way SST impacts corals is a matter of debate among scientific community. Some studies indicate that the extension rates in corals decreased as a result of increase in SST (Carricart-Ganivet, 2004; Cooper et al., 2008; De'ath et al., 2009). Species of genus *Porites* from the Great Barrier Reef (GBR) experienced 16 % decline in extension rates due to a thermal stress (Cooper et al., 2008). Extension rates in *Porites* decreased 1.02 % yr^{-1} from 1988 to 2003 as a result of rise in SST. Decreasing trends in extension rates as a result of increase in SST were measured in *Montastraea annularis* from 6 locations from across the Gulf of Mexico (Carricart-Ganivet, 2004). Other studies concluded that the extension rates increased with the increasing SST (Shinn et al., 1966; Dodge and Lang, 1983). Dodge and Lang (1983) found that the extension rates in *M. annularis* from the Gulf of Mexico increased as a result of increase in SST. Some scientists established that SST had no significant correlation with coral extension rates (Gladfelter et al., 1978; Bak et al., 2009, Helmle et al., 2011). Helmle et al. (2011) found no significant correlation between the extension rates in *M. faveolata* from Florida Keys and annual SST. Their study concluded that *M. faveolata* may have sacrificed skeletal density in order to achieve greater extension in a phenomenon called "stretching modulation of skeletal growth"

(Carricart-Ganivet, 2004). Hypothetically this phenomenon enables corals to compete for space in subtropical waters. However, more study is needed to verify this claim.

The purpose of this study is to measure coral linear extension rates and compare them to SST and other environmental parameters in order to determine the environmental factors that affect the linear extension in corals. Five cores were collected from living coral heads in the Dry Tortugas National Park (DTNP) in August of 2008. The extension rates in *Montastraea faveolata* and *S. siderea* were measured from 1889 to 2007 and in *D. strigosa* from 1954 to 2007. Correlations were made between coral extension rates and SST, sea-level (SL) anomaly, Multivariate El Nino Southern Oscillation Index (MEI), and Atlantic Multidecadal Oscillation (AMO) anomaly. Based on the previous studies (Buddemeier et al., 1974; Tomascik, 1990; Logan et al., 1994) it has been hypothesized that the linear extension in corals is species-specific. The relationship between the extension rate and SST was difficult to predict as previous studies produced conflicting results on the role of SST in coral extension. Lack of studies on ENSO impact on Atlantic corals makes it difficult to speculate what effect ENSO could have on corals from DTNP. Since Helmle et al., (2011) found no significant correlation between AMO and coral extension rates in Florida Keys we expect similar results with corals from DTNP. Even though there is no study done on coral extension rates in conjunction with the SL rise it is established that the SL may affect coral growth indirectly through sedimentation and reduced light levels (Hubbard et al., 2008).

STUDY SITE

Coral cores were collected from the Pulaski Shoal and the Middle Key, Dry Tortugas National Park (DTNP; Figure 1; Table 1) located 112.9 km west of the Key West (http://www.nps.gov/drto/index.htm), the closest human settlement to the park. Dry Tortugas form an elliptical atoll-like structure that is 27 km along the major axis (southwest-northeast) and 12 km along the minor axis (Davis, 1982). The 3 major banks, Pulaski Shoal (NE), Long Key (S), and Loggerhead Key (W) are separated by 10-20 m deep channels. The average depth of the banks is 2-3 m and they are surrounded by 12-23 m deep lagoons. There are 7 islands on Dry Tortugas: Loggerhead, Garden, Bush, Long, Hospital, Middle, and East Keys. Most of the islands are continually above the sea-level, except the Middle Key which is frequently awash and the Hospital Key which is under water during Spring tides.

The Dry Tortugas is located between Florida Shelf to the north and Florida Straights to the south. The Holocene reefs composing the Dry Tortugas are situated on the South Florida margin and occupy transitional zone between south- and east-facing rimmed margin and west-facing ramp margin (Mallinson et al., 2003). The reefs are approximately 14 m thick and are composed mostly of massive corals *Montastraea* spp.. They are situated on the Key Largo Limestone platform composed of older (~125 ka) massive coral heads.

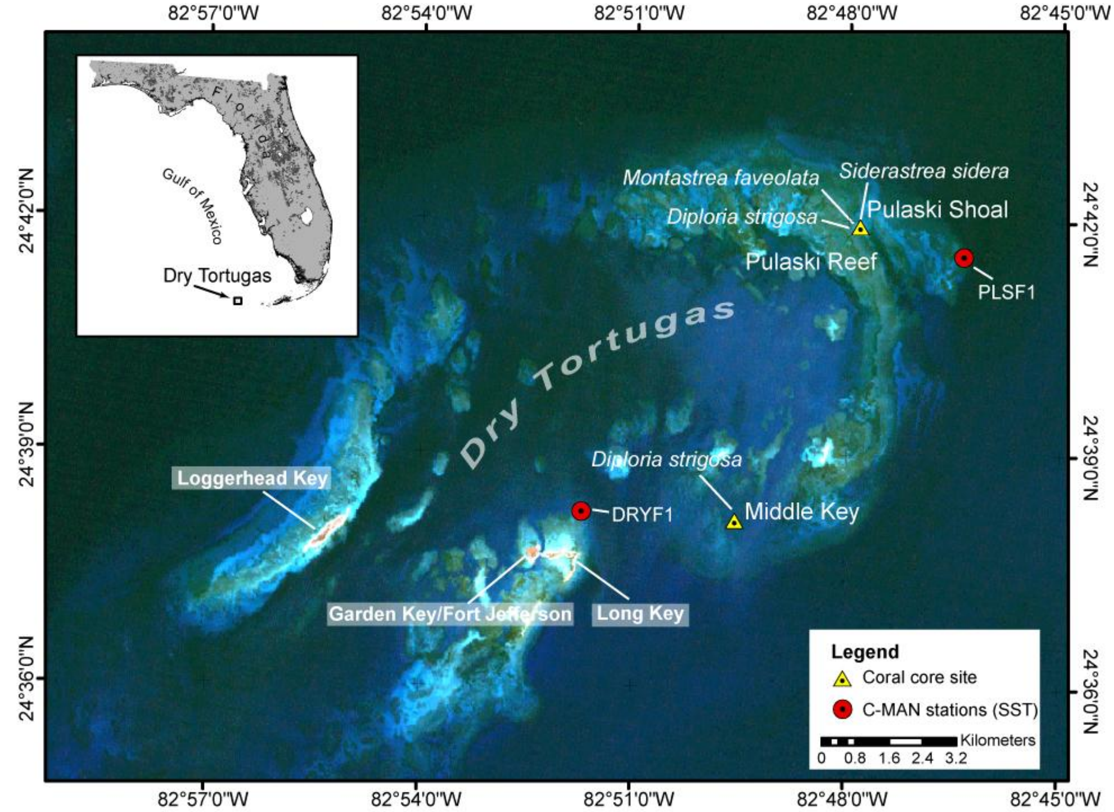

Figure 1. The map is showing DTNP. The yellow triangles represent Pulaski Shoal and Middle Key from where the coral cores were taken. Only 1 core was taken from Middle Key (*Diploria strigosa*). The map is produced by USGS.

METHODS

Coral cores were obtained from live coral heads collected at water depths that ranged from 3.4 to 4.3 m (Table 1) in August of 2008 using the United States Geological Survey (USGS) rotary hydraulic coring system. The equipment for drilling included hydraulic-powered submersible drill, a 10 cm diameter by 61 cm long core barrel with surface set diamond bit, and a hydraulic power unit operated from the boat. Corals were drilled along the vertical growth axis. Following drilling cores were placed on drying table, placed in plastic, and secured for travel. They were taken to the USGS Coastal and Marine Science Center in St. Petersburg, Florida where they were cut into 5 mm thick slabs along the growth axes. Slabs were x-rayed at Louisiana State University by AGFA CR 35-X machine. The distance of the slabs from the beam was not measured but it was uniform for all the slabs. The ruler was positioned on the side of each slab on the x-ray to facilitate calibration. The x-ray images were converted into Photoshop files with 100 pixel cm^{-1} resolution.

The extension rate measurements were made on coral x-ray images using measuring tool (cm) in Photoshop. Measurements were made along the thecal wall, a part of the skeleton where coral calcium carbonate is deposited and coral high and low bands distinguished. Couplet of high and low density bands represented one year interval of growth. Linear distance (cm) between the tops of successive high density bands was measured. Since the high density bands are formed during the late summer and early fall a coral year does not correspond to a calendar year. For the consistency in comparisons to other parameters it is assumed that each coral year starts on the 1st day of September.

Eight slabs from 5 colonies were analyzed (Table 2). (The nomenclature for cores and slabs used in this text is found in Table 2.) At least 3 linear extension transects for each year were measured from each slab; not all of the paths from each slab were measured. In an effort to reduce the measuring errors paths that had clearly visible high and low density bands were chosen over those with less clear banding. Cores were of varying lengths (Table 1) so the time intervals differed among them (Table 2). The shortest core was *Diploria strigosa* MK-A1 (1973-2007) followed by *D. strigosa* PS-C1 (1954-2007), and *Montastraea faveolata* PS-C2 (1939-2007). The longest cores were *M. faveolata* PS-B3 (1889-2007), and *Siderastraea siderea* PS-A1 (1889-2007).

Table 1. Summary of data for each core collected at DTNP, including dates, site and reef names, location (latitude and longitude), depth from which each coral was taken, and core length.

Core	Date Collected	Reef Name	Coral Species	Latitude (N)	Longitude (W)	Water Depth (m)	Core Length (cm)
PS-B3	08/07/08	Pulaski Shoal	*Montastraea faveolata*	24° 41’ 54.852”	-82° 47’ 55.032”	3.4	142
PS-C2	08/08/08	Pulaski Shoal	*Montastraea faveolata*	24° 41’ 40.56”	-82° 47’ 41.64”	3.7	156
PS-C1	08/07/08	Pulaski Shoal	*Diploria strigosa*	24° 41’ 55.938”	-82° 47’ 53.16”	3.4	60
MK-A1	08/06/08	Middle Key	*Diploria strigosa*	24° 38’ 43.08”	-82° 49’ 55.38”	3.4	23
PS-A1	08/06/08	Pulaski Shoal	*Siderastrea siderea*	24° 41’ 55.788”	-82° 47’ 50.82”	4.3	113

Years on the images of coral x-rays were counted backwards from 2008 down core. Year 2008 was not included in the analyses since the high density band was not formed at the time of collection. Statistical calculations were made using Microsoft Office Excel 2010 by applying standard statistical procedures for average, and standard deviation. Correlations between coral extension rates and SST and coral extension rate anomalies and SL anomaly, MEI, and AMO anomaly were made using Pearson product moment correlation coefficient (r) with 95 % confidence interval (α=0.05). The extension rate anomalies were calculated by subtracting the average extension rate of each year from the average extension rate of the entire core.

Table 2. Eight slabs from 5 cores were used in this study. Cores with more than 1 slab have the slabs numbered. Only 2 cores span the entire 119-year record while the length of other cores varies. The number of paths depended on clarity and length of a slab.

Species	Core	Slab	Years	Number of Paths
Montastraea faveolata	PS-B3	1	1889-1962	20
		2	1961-2007	8
		4	1962-2007	18
	PS-C2		1939-2007	25
Diploria strigosa	PS-C1		1954-2007	13
	MK-A1		1973-2007	11
Siderastrea siderea	PS-A1	1	1944-2007	16
		2	1889-2007	26

RESULTS

In considering the results it should be noted that there was a possibility of measuring errors when designating starting and ending point of each band. This is especially the case with *Siderastrea siderea* PS-A1 that deposits its calcium carbonate more evenly throughout the year causing high and low density bands to be less distinctive than in the other two species. To reduce this error the extension rates of all the paths were measured 3 times and the third time was used in further analyses. It has been observed that the *Montastraea faveolata* polyps tend to have meandering paths which makes the paths grow at an angle. Consequently the paths that grew at an angle may appear shorter or longer on the x-ray than they actually are, leading to the incorrect measurements. To reduce this error, the paths were measured until they start meandering, at which point another path would be chosen for measuring.

Montastraea faveolata had the highest average extension rate and variability of all three species in this study (Figure 2-5; Table 3). The average extension rate and variability in *Diploria strigosa* were lower than those of *M. faveolata* but its average extension rate was higher than in *Siderastraea siderea*. Variability was greater in *S. siderea* than in *D. strigosa* which is reflected in a higher annual extension rate range, higher standard deviation, and higher coefficient of variation in *S. siderea* than in *D. strigosa*.

Table 3. Average annual extension rates with standard deviation, number of samples, extension rate range, and coefficient of variation for 5 coral colonies. Note the differences between the colonies of the same and different species.

Coral Core	Average Annual Extension (cm) ± Standard deviation (cm)	Average Annual Extension Rate Range (cm)	Coefficient of variation (CV)
Diploria strigosa PS-C1	0.73±0.06 (n=54)	0.62 to 0.86 (range=0.24)	0.08
Diploria strigosa MK-A1	0.59±0.05 (n=35)	0.49 to 0.75 (range=0.26)	0.08
Siderastrea siderea PS-A1	0.42±0.06 (n=183)	0.30 to 0.60 (range=0.30)	0.14
Montastraea faveolata PS-B3	0.84±0.14 (n=165)	0.53 to 1.22 (range=0.69)	0.17
Montastraea faveolata PS-C2	0.67±0.08 (n=69)	0.47 to 0.82 (range=0.35)	0.12

There was a significant correlation between slabs cut from the same core (Figure 6) for both *Montastraea faveolata* PS-B3 (r=0.82, P<0.0001) and *Siderastrea siderea* PS-A1 (r=0.74, P<0.0001). No significant correlation in trend was found between the two *Diploria strigosa* cores (r=-0.10, P=0.5676). *Diploria strigosa* MK-A1 had a lower average extension rate than *D. strigosa* PS-C1. There was a significant positive correlation in trends between *M. faveolata* PS-B3 and *M. faveolata* PS-C2 (r=0.34, P=0.0043) even though *M. faveolata* PS-C2 had lower average extension rates than *M. faveolata* PS-B3 (Figure 7; Table 3). An inverse correlation in extension rate trends was found between *M. faveolata* PS-B3 and *S. siderea* PS-A1 (Figure 8; Table 4).

Siderastrea siderea PS-A1 had an overall increasing trend (r=0.64, P<0.0001) in the extension rates from 1889 to 2007, while *M. faveolata* PS-B3 had a significant decreasing trend (r=-0.22, P=0.0162) for the same time interval. Other cores showed no significant overall trends (Table 5; Figure 2-5, 9). Apart from the overall trends, trends for certain parts of the record were present in all cores. Only *Siderastrea siderea* PS-A1 had a significant correlation with annual and warmest month SST (Figure 10; Table 6) and MEI (Figure 13; Table 7) while both long cores *M. faveolata* PS-B3 and *S. siderea* PS-A1 had low and insignificant correlations with AMO (Table 7). The Key West SL anomaly had a significant positive correlation with the extension rates of *Siderastrea siderea* PS-A1 (r=0.73, P<0.0001; Figure 11, 12; Table 7) and *Montastraea faveolata* PS-C2 (r=0.32, P=0.0091; Figure 11, 12; Table 7)

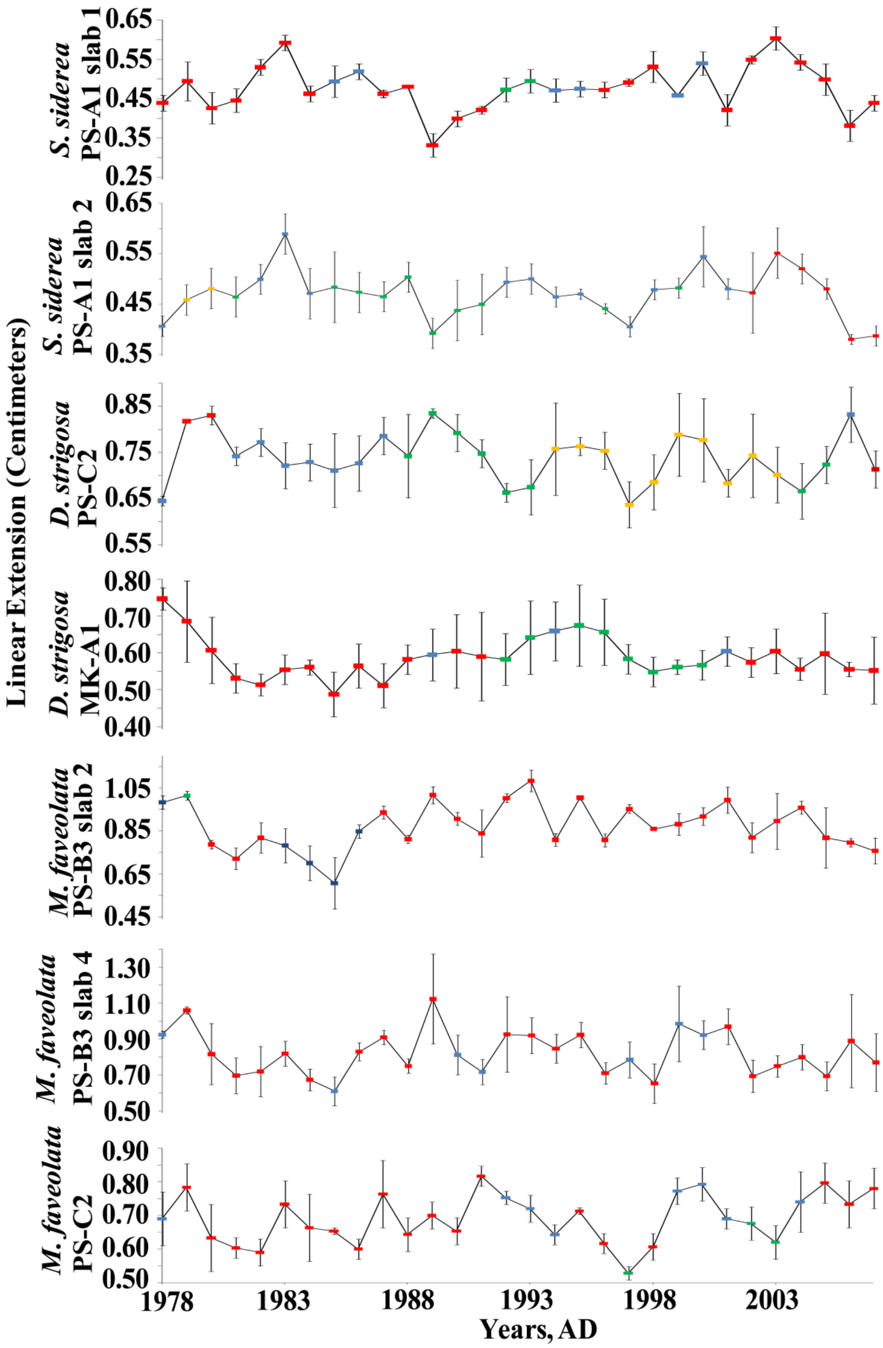

Figure 2. Average annual extension rates for the period from 1978 to 2007 with standard deviation bars. Number of samples for each year is color coded: red (3 samples), blue (4 samples), green (5 samples), and yellow (6 samples). Y-axis scales were adjusted to show variability.

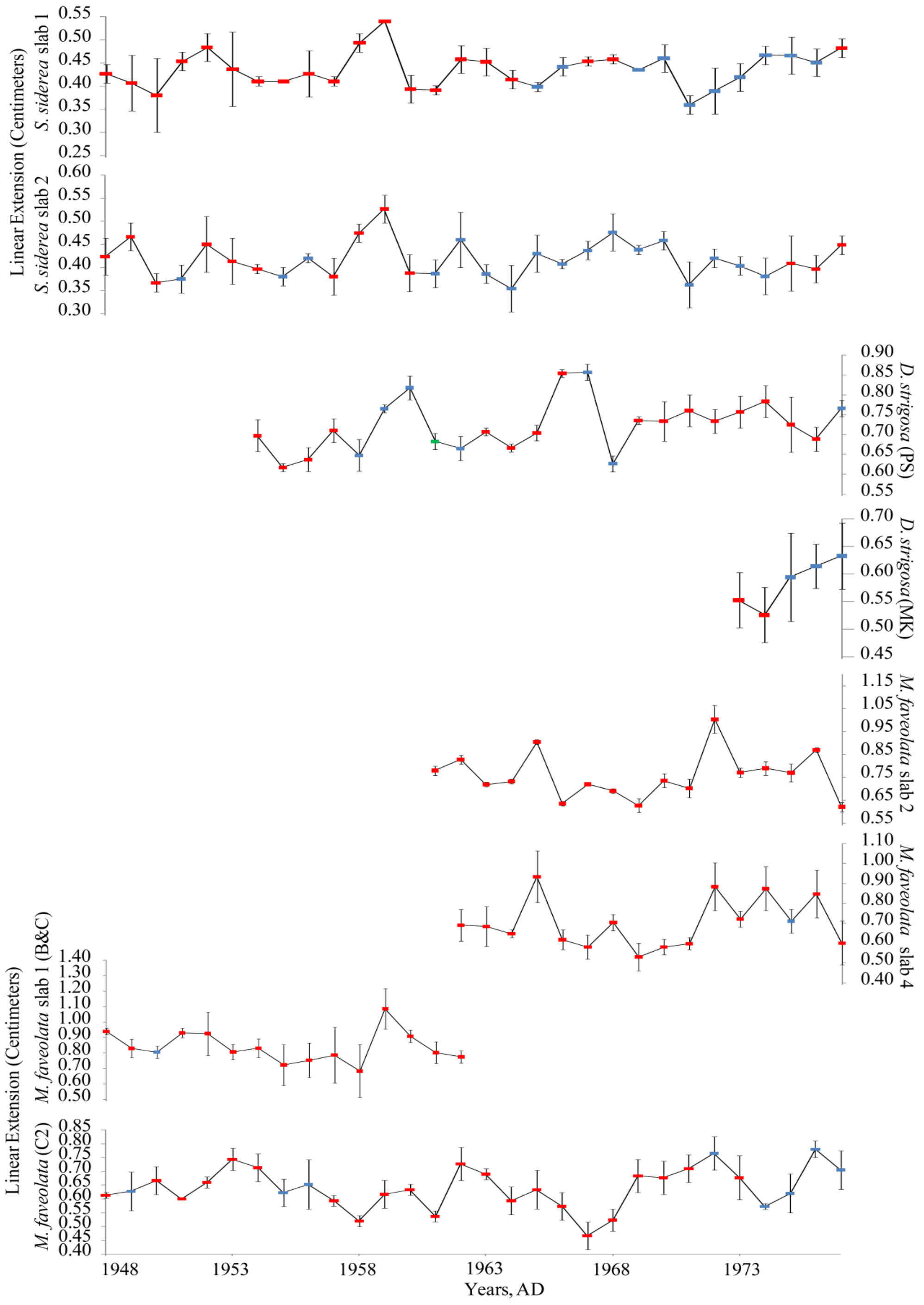

Figure 3. Average annual extension rates for the period from 1948 to 1977 with standard deviation bars. Number of samples for each year is color coded: red (3 samples), blue (4 samples), green (5 samples), and yellow (6 samples). Y-axis scales were adjusted to show variability.

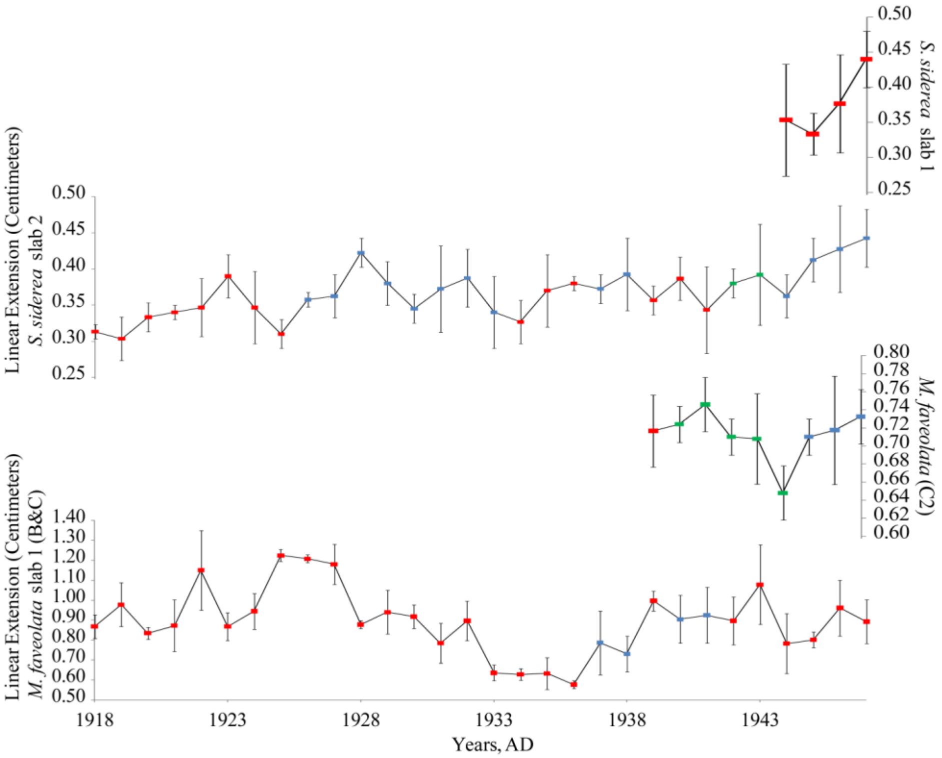

Figure 4. Average annual extension rates for the period from 1918 to 1947 with standard deviation bars. Number of samples for each year is color coded: red (3 samples), blue (4 samples), green (5 samples), and yellow (6 samples). Y-axis scales were adjusted to show variability.

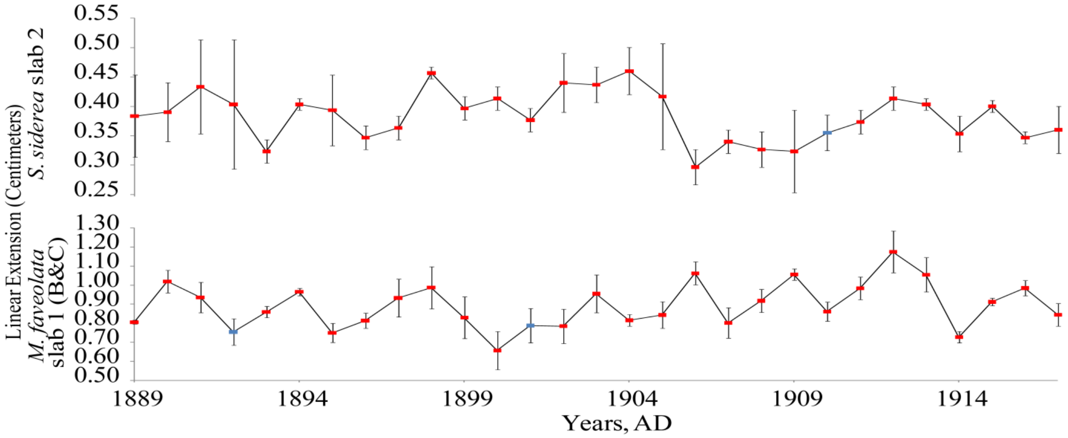

Figure 5. Average annual extension rates for the period from 1889 to 1917 with standard deviation bars. Number of samples for each year is color coded: red (3 samples), blue (4 samples), green (5 samples), and yellow (6 samples). Y-axis scales were adjusted to show variability.

DISCUSSION

The extension rates in corals varied among the slabs, cores, and species. Correlation between the slabs of the same core was high in *Montastraea faveolata* PS-B3 slabs 2 and 4 ($r=0.82$, $P<0.0001$) and *Siderastrea siderea* PS-A1 slabs 1 and 2 ($r=0.74$, $P<0.0001$; Figure 6). Correlation between the slabs that grew in the same colony was higher than that of the same-species slabs from different colonies. It is likely that the high degree of similarity in the extension rates in the slabs from the same colony is a factor of genetics given that the polyps are clones of each other possessing the identical genetic makeup and hence respond to the external environment in a similar way (Oliver, 1968). As the external environment is essentially identical for most polyps within the core it is not surprising that their extension rates had such a high correlation.

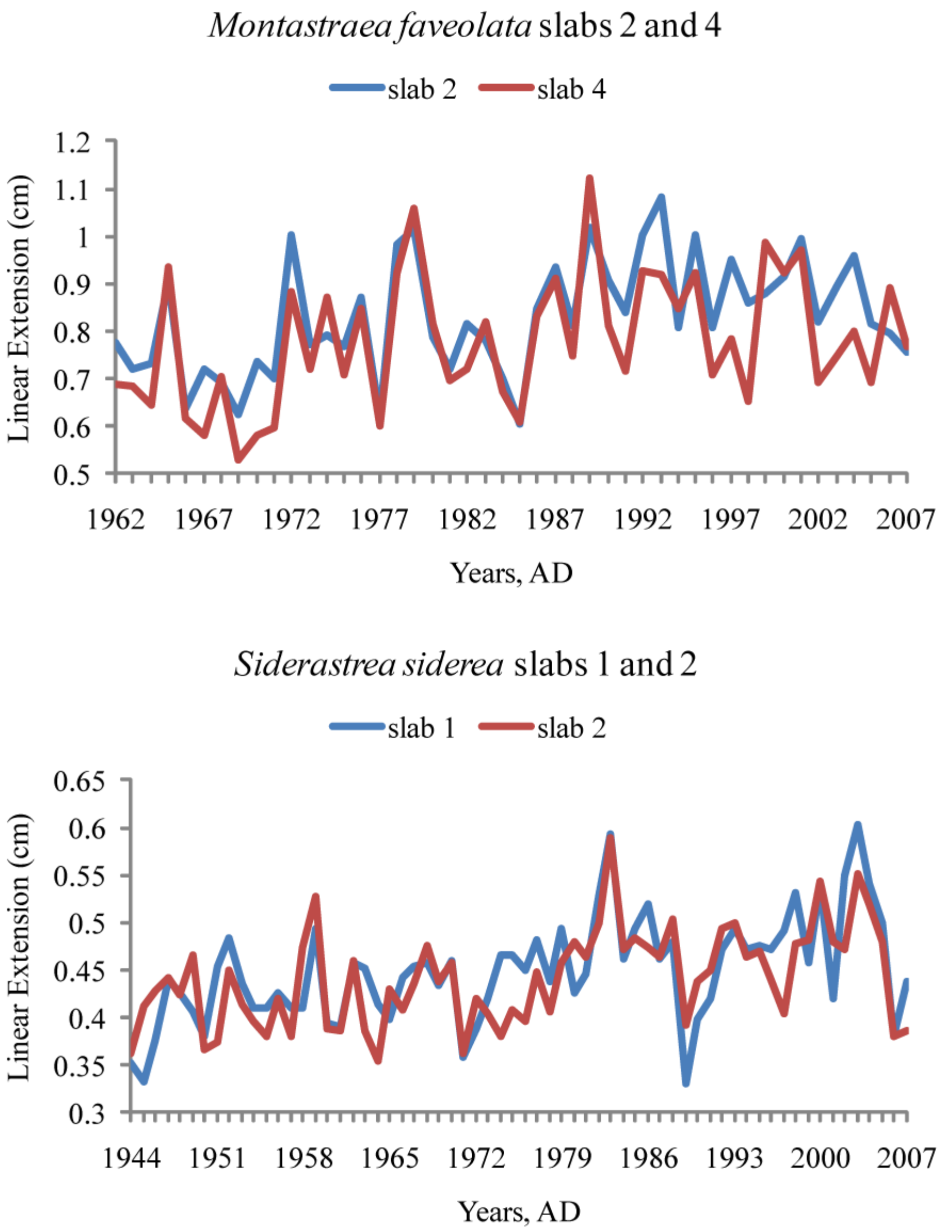

Figure 6. There was a high correlation between the slabs obtained from the same core. At the top is *Montastraea faveolata* PS-B3 slab 1 and 4 and at the bottom is *Siderastrea siderea* PS-A1 slab 1 and 2.

Even though the two cores had a significant positive correlation with each other (r=0.34, P=0.0043), *Montastraea faveolata* PS-B3 had 25.37 % higher average extension rate than *M. faveolata* PS-C2. Although statistically *M. faveolata* PS-B3 showed decreasing trend over time while *M. faveolata* PS-C2 showed no trend (Table 5), the general pattern showed decreasing trend in both cores until the late 1960s after which the extension rates in both cores stabilized (Figure 7). It is likely that the two cores of *M. faveolata* experienced similar environmental conditions as they were collected from the same reef patch and similar water depth (~3.5 m; Table 3). High correlation in extension rates between these two cores suggests that the extension rate trend was influenced by the prevailing environmental conditions while their average extension rate was affected by local conditions (Heiss, 1996) and biological factors (Oliver, 1968).

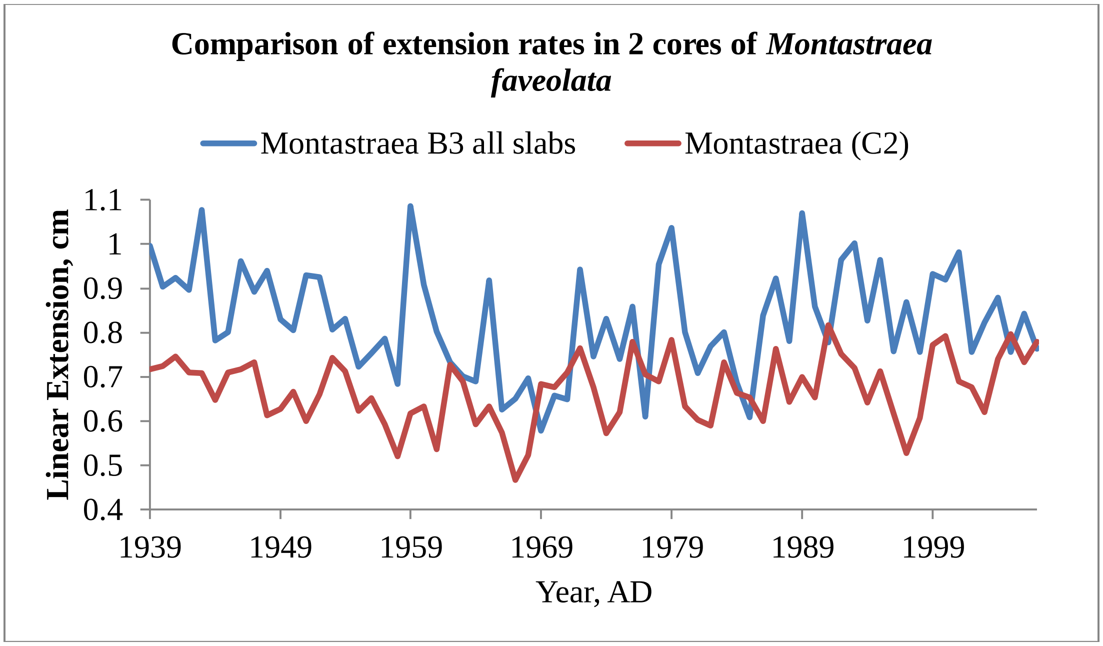

Figure 7. The correlation between *Montastraea faveolata* PS-B3 and PS-C2 core was statistically significant although *M. faveolata* PS-B3 had a decreasing trend while *M. faveolata* PS-C2 showed no trend over time. The relative shortness of *M. faveolata* PS-C2 could explain the lack of trend in this core since the FIGURE shows similarities between the two cores.

Diploria strigosa PS-C1 had 21.21 % higher average extension rate than *D. strigosa* MK-A1 (TABLE 3) and no similar trends or correlations were observed between the two *D. strigosa* cores (r=-0.10, P=0.5676; Table 5). The x-rays of *Diploria strigosa* PS-C1 revealed that the coral had hyperplasia tumor which typically increases coral cell growth leading to abnormally high extension rates as observed in this core (Gateno et al., 2003). *Diploria strigosa* MK-A1 extension rates were closer to those found elsewhere in the Caribbean Sea and the Gulf of Mexico suggesting a normal growth (Logan et al., 1994). The lack of common pattern or significant correlation between the extension rates of *D. strigosa* cores suggests that the prevailing influences on these two cores were not the same. It is likely that *D. strigosa* MK-A1 experienced normal extension rate under a number of environmental and biological factors while *D. strigosa* PS-C1 was affected by a tumor that altered its growth pattern and caused it to grow abnormally.

In agreement with other studies the extension rates in our cores were species-specific (Buddemeier et al., 1974; Tomascik, 1990; Logan et al., 1994). The average extension rates of *Montastraea faveolata* cores (0.67 and 0.84 cm yr^{-1}) were within the range for the species and similar to that found in other studies (Carricart-Ganivet et al., 2000; Helmle et al., 2011). Studies from across the Caribbean Sea measured the average extension rates in *M. faveolata* to range from as low as 0.38 cm yr^{-1} in Discovery Bay, Jamaica (Dustan, 1975) to as high as 0.76 cm yr^{-1} in Belize (Graus and Macintyre, 1982), 0.87 cm yr^{-1} in Mexican Caribbean (Carricart-Ganivet et al., 2000), 0.91 cm yr^{-1} in U.S. Virgin Islands (Baker and Weber, 1975), and 0.98 cm yr^{-1} in U.S. Virgin Islands (Dodge and Brass, 1984).

The extension rates of 0.59 cm yr^{-1} and 0.73 cm yr^{-1} in *Diploria strigosa* cores were above the average but were still within the range for the species. The extension rates found in various locations across the West Atlantic measured 0.46-0.59 cm yr^{-1} in

Panama (Guzman and Cortes, 1989), 0.43-0.46 cm yr^{-1} in Aruba (Harriot, 1992), 0.35-1.00 cm yr^{-1} in Bahamas (Hubbard and Scaturo, 1985), 0.5 cm yr^{-1} in East Flower Banks (Hudson et al., 1994), and 0.33 cm yr^{-1} in Bermuda (Johannes et al., 1983). Of all the three species in this study *Siderastrea siderea* PS-A1 had the lowest extension rates (0.42 cm yr^{-1}). Its average extension rate was 0.34 cm yr^{-1} less than in Panama (Guzman and Tudhope, 1998) but comparable to that from Puerto Rico (0.35 to 0.43 cm yr^{-1}; Torres and Morelock, 2002).

Montastraea faveolata PS-B3 correlated significantly but inversely with *Siderastrea siderea* PS-A1 (r=-0.19, P=0.0385; Figure 8; Table 4) and positively with *Diploria strigosa* MK-A1 (r=0.41, P=0.0144; Table 4). This suggests that the fast-growing *M. faveolata* and *D. strigosa* had similar responses to environmental conditions in contrast with the slow-growing *S. siderea*. The growth strategies among the species may have contributed to their different responses to environmental challenges and producing opposite results in the extension rates. For example, in a study from Puerto Rico *S. siderea* was found to be nonsensitive to sedimentation while *M. annularis* was highly intolerant of sedimentation (Torres and Morelock, 2002). Consequently, the extension rates in *M. annularis* decreased as a result of increased suspended matter in a water column while the extension rates in *S. siderea* remained unaffected. This implies that corals species may respond differently when affected by a similar environmental conditions. Although the study focused on sedimentation it is conceivable that corals may respond differently to other environmental conditions as well, including SST. Local environmental factors on the reefs may cause the extension rate to vary even in corals that live in close proximity to each other (Heiss, 1996).

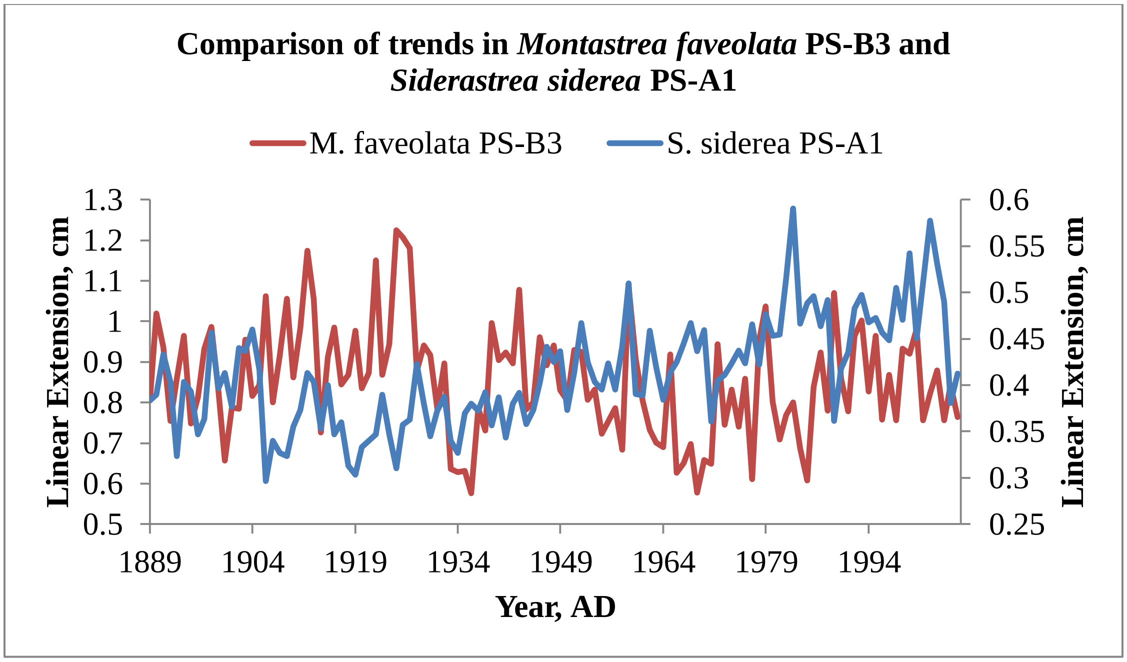

Figure 8. The correlation between *M. faveolata* PS-B3 and *S. siderea* PS-A1 was significant but negative. This can be observed on the FIGURE. On the right side is the scale for *S. siderea* extension rates and on the left for *M. faveolata*.

Table 4. Correlation (r) between each core. The bold numbers represent cases with significant correlation. Long *Montastraea faveolata* record had significant correlation with *Siderastrea siderea* PS-A1, *Diploria strigosa* MK-A1, and *M. faveolata* PS-C2.

Core	PS-C1	MK-A1	PS-B3	PS-C2
PS-A1	r=-0.07 (df=52, P=0.6150)	r=-0.14 (df=33, P=0.4225)	**r=-0.19 (df=117, P=0.0385)**	r=0.01 (df=67, P=0.9350)
PS-C1	-	r=-0.10 (df=33, P=0.5676)	r=0.09 (df=52, P=0.5175)	r=0.09 (df=52, P=0.5175)
MK-A1	-	-	**r=0.41 (df=33, P=0.0144)**	r=0.14 (df=33, P=0.4225)
PS-B3	-	-	-	**r=0.34 (df=67, P=0.0043)**

Some species of corals were thought to experience the phenomenon called "stretching modulation of skeletal growth." Carricart-Ganivet (2004) proposed that

Montastraea faveolata may sacrifice its density to achieve higher extension rate during unfavorable environmental conditions, a strategy used to compete for space. Other coral species may engage in this strategy as well but due to the lack of evidence it is unknown whether or not *Siderastrea siderea* or *Diploria strigosa* are capable of sacrificing density to increase their linear extension. The extension rates of *S. siderea* in this study were in a lower range for the species while the other two species experienced above average extension rates. This implies that *M. faveolata* and *D. strigosa* have similar strategies to cope with the changing environment in contrast with *S. siderea*. However, since density of the slabs was not measured it can only be speculated that *M. faveolata* and *D. strigosa* compensated for their high extension rates by reducing their skeletal density.

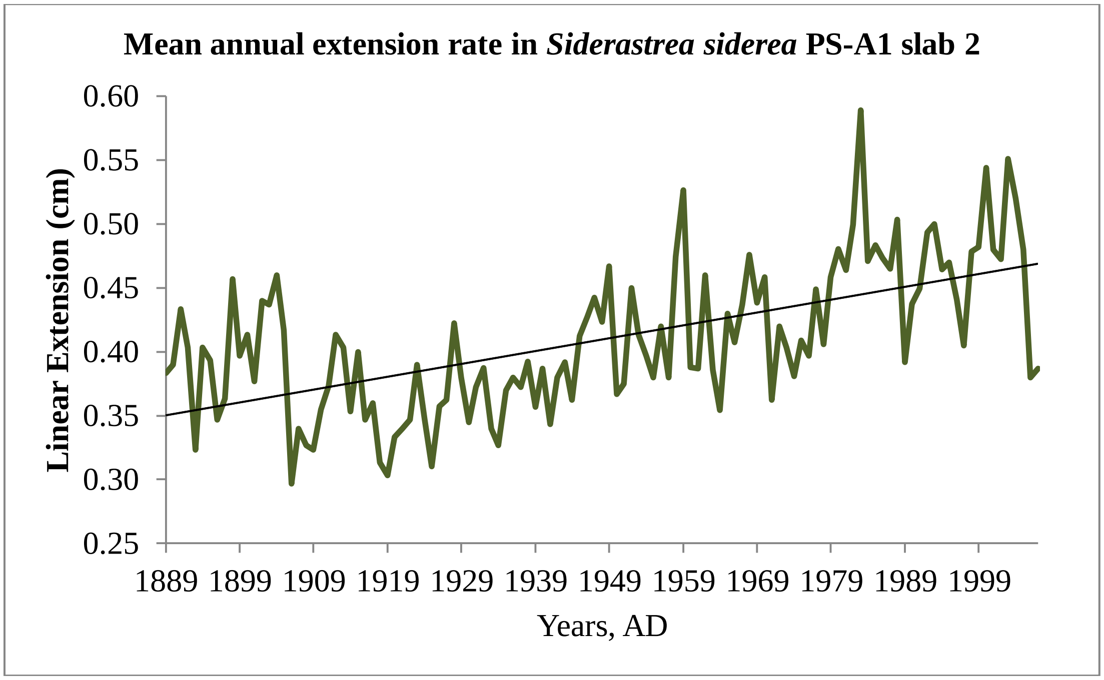

Figure 9. Average annual linear extension rate in *Siderastrea siderea* PS-A1 slab 2 from 1889 to 2007. The linear regression equation and r value are shown on the graph as a function of linear extension over time.

Table 5. Extension rates varied over a time. Significant trends were measured in 2 cores (bold) while others showed no trend.

Coral slab	r values	df	P-value
Siderastrea siderea PS-A1	**0.64**	**117**	**P<0.0001**
Diploria strigosa PS-C1	0.15	52	P=0.2790
Diploria strigosa MK-A1	-0.05	33	P=0.7755
Montastraea faveolata PS-B3	**-0.22**	**117**	**P=0.0162**
Montastraea faveolata PS-C2	0.17	67	P=0.1626

Several studies proposed that SST is a leading cause of extension rate variability in corals (Shin et al., 1966; Carricart-Ganivet, 2004; De'ath et al., 2009). There were three temperature data sets available to us for the area near our coral locations: local buoy SST, Key West air temperature, and The International Comprehensive Ocean-Atmosphere Data Set (ICOADS) SST. Local buoy data sets were collected from stations C-MAN PLSF1 (24°41'36" N 82°46'24" W) and C-MAN DRYF1 (24°38'18" N 82°51'42" W; Figure 1). Both stations are located within the boundaries of DTNP (PLSF1 was located at Pulaski Shoal near the locations where most of our corals were collected). All buoy values were obtained hourly and were computed into monthly and annual SST values. Five complete years were available for annual comparisons, 9 years of warmest month averages, and 10 years of coldest month averages, making this record the shortest of all 3 records available. The second record considered was the Key West air temperature. The air temperature was recorded daily by volunteers and the sensors were maintained by National Weather Service (http://www.nc-climate.ncsu.edu/cronos/?station=084570&temporal=hourly). Temperature was measured

1.22 m above the sea level at the Key West International Airport (station 084570) for the period from 1895 to 2007. The third record available for DTNP area was ICOADS SST that was obtained from NOAA. ICOADS contains observations by ships and buoys and is considered by NOAA to be one of the most complete and heterogeneous collections of SST (http://icoads.noaa.gov/). ICOADS contains the SST for the past 300 years and is arranged in 2° latitude by 2° longitude boxes prior to 1959 and 1° by 1° since 1960. The grids used in this study were centered on 82°30' W and 24°30' N.

Although the local buoys were very close to the locations of our corals and produced the most reliable records available they are relatively short when compared to coral extension records. However, since the buoy data were not incorporated into ICOADS or Key West datasets, buoy data were used to validate ICOADS and the Key West data. When compared to ICOADS SST, buoy records had a significant correlation with ICOADS warmest month ($r=0.92$, $P=0.0004$), coldest month ($r=0.86$, $P=0.0014$), monthly ($r=0.98$, $P<0.0001$), and annual SST ($r=0.83$, $P=0.0409$). Nonetheless, it should be acknowledged that more data were available in recent years for the construction of ICOADS SST than 100 years ago and prior to year 1960 the data for ICOADS was arranged in 2° latitude by 2° longitude instead of 1° by 1° thereafter. Because of this, buoys can validate ICOADS for recent years but one should be cautious when using it for the interval prior to 1960. The buoys had a significant correlation with the Key West warmest month ($r=0.74$, $P=0.0226$) and monthly ($r=0.93$, $P<0.0001$) air temperature but not with the coldest month ($r=0.38$, $P=0.2787$) and annual ($r=0.11$, $P=0.7081$) temperature. Since the buoy SST had higher correlation with the ICOADS SST data than the Key West air temperature the ICOADS SST was chosen to correlate it with the coral extension rates. Gridded SST datasets such as ICOADS are widely used in coral studies adding to its legitimacy (Guzman et al., 2008; Payet and Agricole, 2006, Vargas-Angel et al., 2006).

In this study annual ICOADS SST correlated significantly only with *Siderastrea siderea* PS-A1 extension rates (r=0.43, P<0.0001; Figure 10; Table 6) but not with the extension rates of other cores. Slow growing *S. siderea* produced the extension rates that are shorter but steady and responded well to a long-term annual SST trends. The extension rates of the fast-growing *Montastraea faveolata* and *Diploria strigosa* may have been affected by sudden and extreme SST changes since they had no significant correlation with annual SST.

Siderastrea siderea PS-A1 was correlated positively and significantly with the average warmest month SST (r=0.56, P<0.0001; Figure 10; Table 6) but not with the coldest month. This agrees with the study by Carricart-Ganivet (2004) who found that *M. annularis* from the Gulf of Mexico was affected by maximum SST while unaffected by minimum SST. Since correlations between the extension rates in corals and SST were positive, our study suggests that the warm summer and annual SST enhance the extension of coral skeleton in *S. siderea* from DTNP. This agrees with earlier studies on *Acropora palmata* and *M. annularis* from Florida Keys (Shinn et al., 1966; Dodge and Lang, 1983) where they found that the extension rates increased with the increasing SST. In another study, species of genus *Porites* was affected by minimum SST but unaffected by maximum SST contradicting our study (Lough and Barnes, 2000).

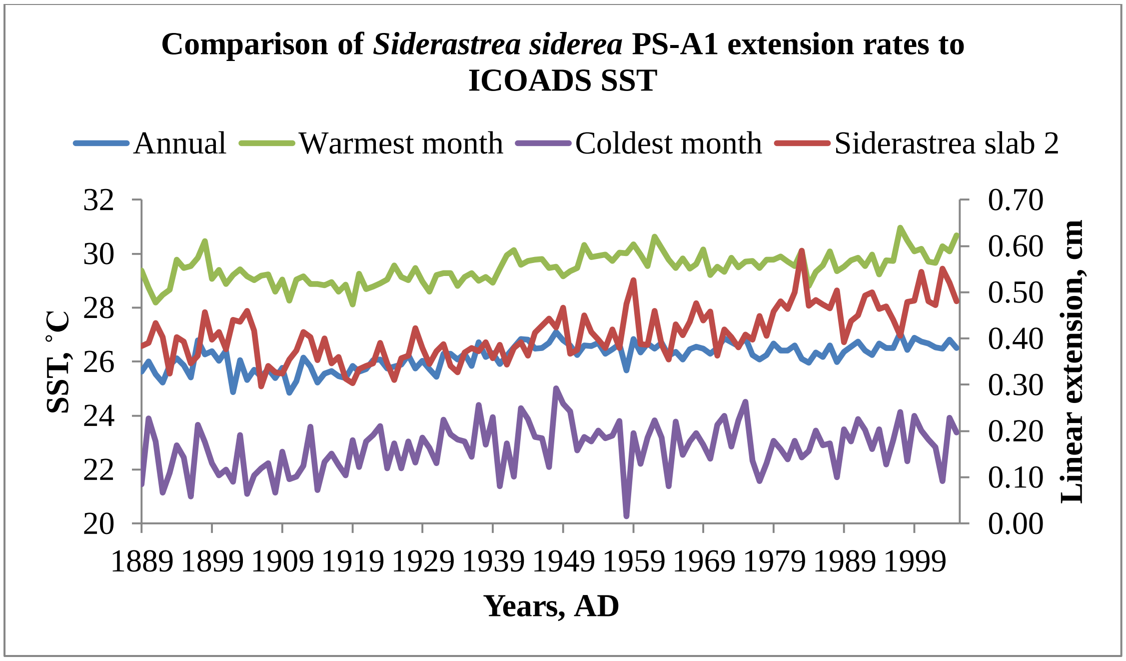

Figure 10. Linear extension rate in *Siderastrea siderea* PS-A1 correlated significantly with annual (r=0.43, P<0.0001) and warmest month SST (r=0.56, P<0.0001), but not with the coldest month (r=0.11, P=0.2377) SST.

Table 6. Presented are r values for each core compared to ICOADS sea-surface temperature, including the average annual, warmest month, and coldest month SST. The bold numbers represent significant correlation when α = 0.05.

Core	ICOADS annual SST	ICOADS warmest month SST	ICOADS coldest month SST
PS-A1	**r=0.43 (df=115, P<0.0001)**	**r=0.56 (df=115, P<0.0001**	r=0.11, (df=115, P=0.2377)
PS-C1	r=0.06 (df=50, P=0.6726)	r=-0.22 (df=50, P=0.1171)	r=0.03 (df=50, P=0.8328)
MK-A1	r=-0.08 (df=31, P=0.6581)	r=-0.02 (df=31, P=0.9120)	r=-0.24 (df=31, P=0.1785)
PS-B3	r=-0.05 (df=115, P=0.5924)	r=-0.13 (df=115, P=0.1624)	r=0.12 (df=115, P=0.1975
PS-C2	r=0.09 (df=65, P=0.4689)	r=0.09 (df=65, P=0.4689)	r=0.10 (df=65, P=0.4207)

In accord with some studies the extension rates of other cores (*Diploria strigosa* PS-C1, *D. strigosa* MK-A1, *Montastraea faveolata* PS-B3, *M. faveolata* PS-C2) had no significant correlation with SST (Table 6). It has been discussed previously that *D.*

strigosa PS-C1 has been affected by hyperplasia tumor which altered its growth patterns. The other *D. strigosa* is a short core (1973-2007) and it is possible that the SST was not a predominant factor that affected the extension rates of *D. strigosa* MK-A1. This core was collected from Middle Key reef implying that the local environmental conditions that affected this core might be somewhat different than at the Pulaski Shoal where all the other cores were collected. Our results agree with Helmle et al. (2011) who found no correlation between *Montastraea faveolata* extension rates and SST from Florida Keys. However, this does not mean that the relationship between SST and extension rates does not exist but that the corals from DTNP were able to adapt to increasing SST (Helmle et al., 2011). As DTNP is a subtropical location SST has not reached the point where it would negatively affect the coral extension rates. In case where SST is not a major stressor other factors may drive the extension rate variability. Corals may also apply various methods to cope with the stressful environment without sacrificing their skeletal extension. Study from Florida Keys speculates that *M. faveolata* may have sacrificed density of their skeleton in order to achieve higher extension rates under unfavorable environmental conditions (Carricart-Ganivet, 2004). Nevertheless, more study is needed to confirm this phenomenon.

Sea level change is another factor that could affect coral extension. The dataset on SL anomalies from the Key West was obtained for a period from 1913 to 2007. The original data was collected by American Meteorological Society and is available at NOAA (http://tidesandcurrents.noaa.gov/sltrends/sltrends.shtml). The monthly SL anomalies were averaged to obtain annual SL anomaly that was compared to coral extension rate anomalies. Local average SL in the Key West has been increasing at the rate of 2.24±0.16 mm yr^{-1} between 1913 and 2006 (http://tidesandcurrents.noaa.gov/sltrends/sltrends_station.shtml?stnid=8724580 Key West, FL). Several factors may contribute to local SL rise, including polar ice melting (Meehl et al., 2005), thermal expansion of the sea water due to the increase in SST that causes decrease in water density, atmospheric pressure (Church and White, 2006), and ocean currents (Levermann et al., 2005). The Key West SL anomalies were compared to the extension rate anomalies in corals and produced a significant positive correlation with the extension rates of *Siderastrea siderea* PS-A1 ($r=0.73$, $P<0.0001$; Figure 11, 12; Table 7) and *Montastraea faveolata* PS-C2 ($r=0.32$, $P=0.0091$; Figure 11, 12; Table 7). Corals use various strategies to cope with the SL change (Hallock, 2005). Drowning of coral reefs have happened in a distant past as a result of rapid SL rise following periods of deglaciation when SL reached 30 to 40 m above the reef crest (Webster et al., 2003, Webster et al., 2004). As these conditions were not present in DTNP it is unclear whether or not the corals were trying to keep up with the slow rise in SL. Since the cores were extracted from ~3.5 m water depth, where they had an abundance of light, there would be no need for them to increase their extension rates in order to survive. On the other hand the increase in SST would have caused the thermal expansion of the sea water and the subsequent rise in SL. Assuming that both the extension rates and the SL were affected by SST, they would have produced a significant correlation despite the fact that they had no direct effect on each other.

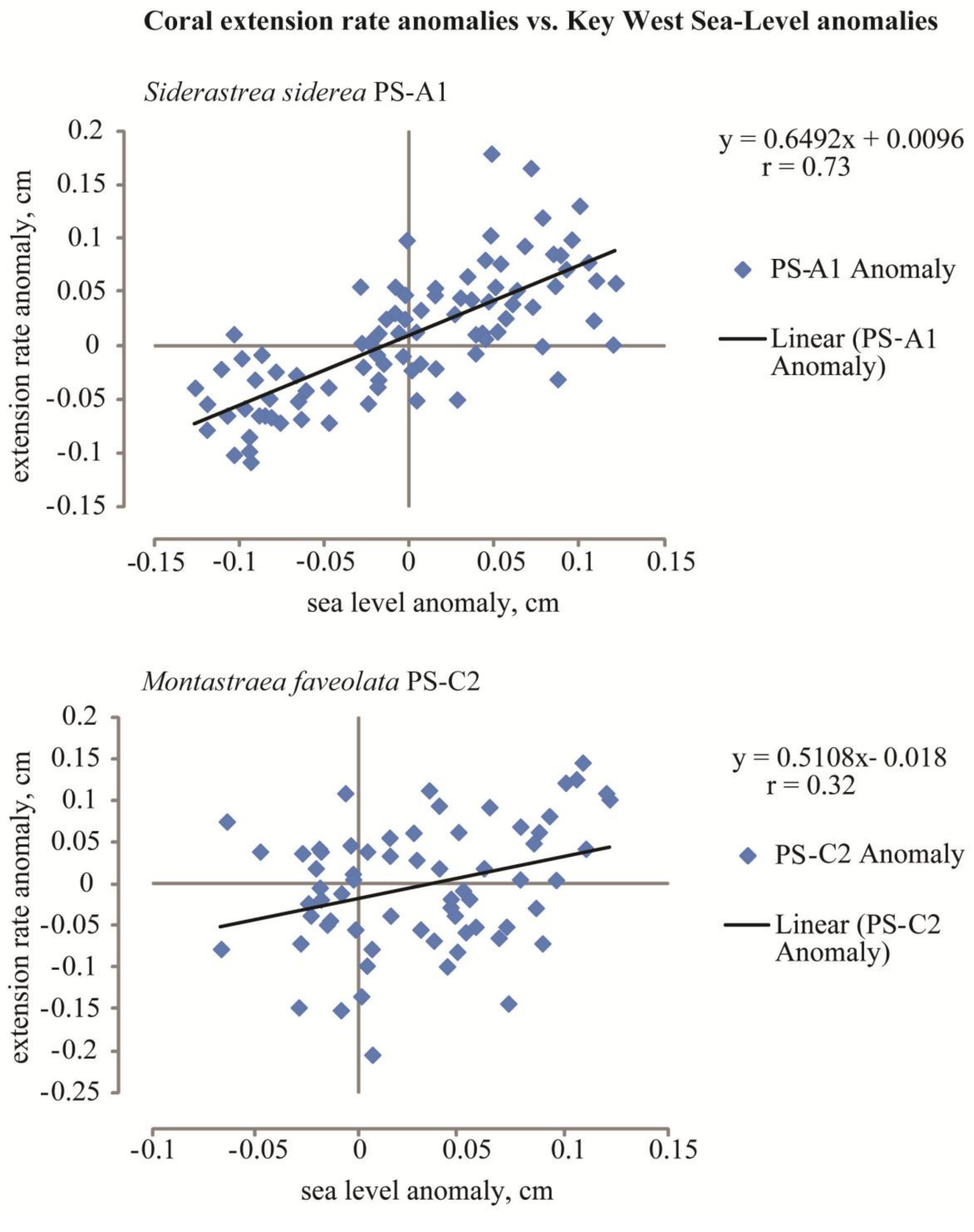

Figure 11. The Key West sea-level anomalies correlated significantly with the extension rate anomalies of *Siderastrea siderea* PS-A1 (r=0.73, P<0.0001) and *Montastraea faveolata* PS-C2 (r=0.32, P=0.0091).

Another hypothetical explanation for correlation between SL and the extension rates is based on the fact that SL leads to resuspension of sediments on the reef and the surrounding seabed and coastal area that could affect light penetration to corals and thus affect coral extension rates. The level of resuspension depends on the seabed roughness, settling characteristics of sediments available, and the type of sediment on the seabed, as well as the availability of fine-grained sediments from coastal plains and deltas (Ogston and Field, 2010). In a study from Molokai, Hawaii by Ogston and Field (2010) it has been proposed that the increase in SL led to resuspension of sediments on the reef which in turn led to the reduction in light level penetration to corals slowing the photosynthesis of zooxanthellae and thus reducing the coral growth. Study by Rogers (1990) demonstrated that the increased sedimentation caused lower extension rates, density, and calcification in corals. As DTNP is located away from any major landmasses, it is difficult to consider that the SL rise would lead to a major increase in suspended particles on the reef. Torres and Morelock (2002) established that *Montastraea faveolata* is a species sensitive to sedimentation while *Siderastrea siderea* is non-sensitive. It would be difficult to consider that resuspension of sediments due to the rise in SL happened at DTNP since both, sensitive and non-sensitive species responded positively to the SL rise. At this point there is no satisfactory explanation as to why the extension rates increased with the increasing SL.

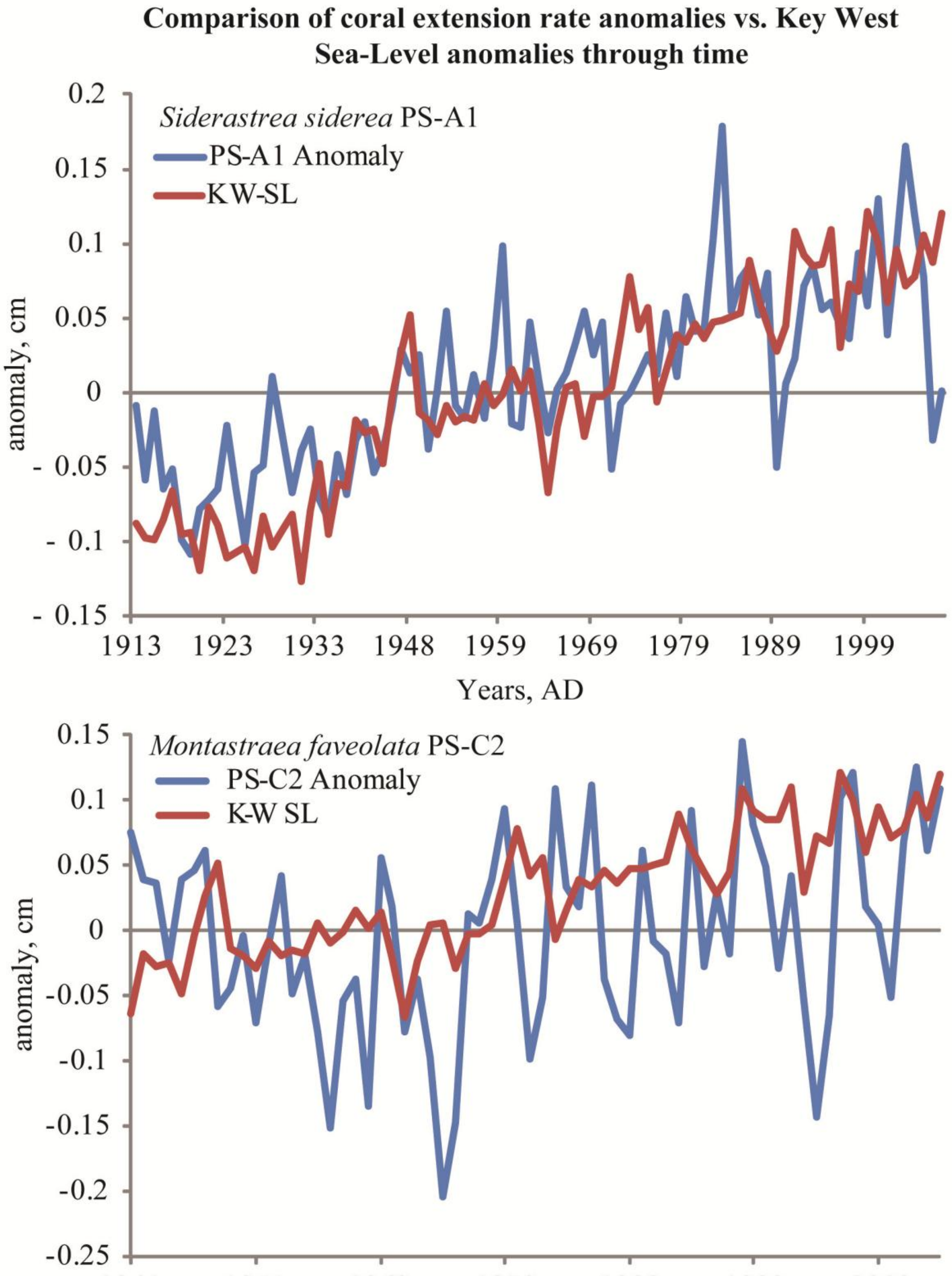

Figure 12. The line graph shows the extension rate sea-level anomaly comparisons through time. Only the two cores shown here had a significant correlation with sea-level.

The extension rate anomalies were compared to MEI that factored in 6 variables: SL pressure, zonal and meridional components of the surface wind, SST, surface air temperature, and total cloudiness fraction of the sky. These variables were collected by ICOADS and used to construct MEI record from 1950 to 2007. Monthly values of global MEI record were averaged to obtain annual index suitable for comparison with annual extension rates. Being derived, in part, from ICOADS SST, MEI showed significant correlation with annual ICOADS SST (r=37, P=0.007) and the extension rate anomalies of *Siderastrea siderea* PS-A1 (r=0.43, P=0.0008; Figure 13; Table 7). It had no significant correlation with the extension rate anomalies of other cores. The high correlation between MEI and *S. siderea* PS-A1 is not surprising given that studies from the Pacific Ocean show strong correlation between ENSO and coral extension rates (Alibert and McCulloch, 1997). The impact of ENSO on Atlantic corals is not well understood due to the lack of studies.

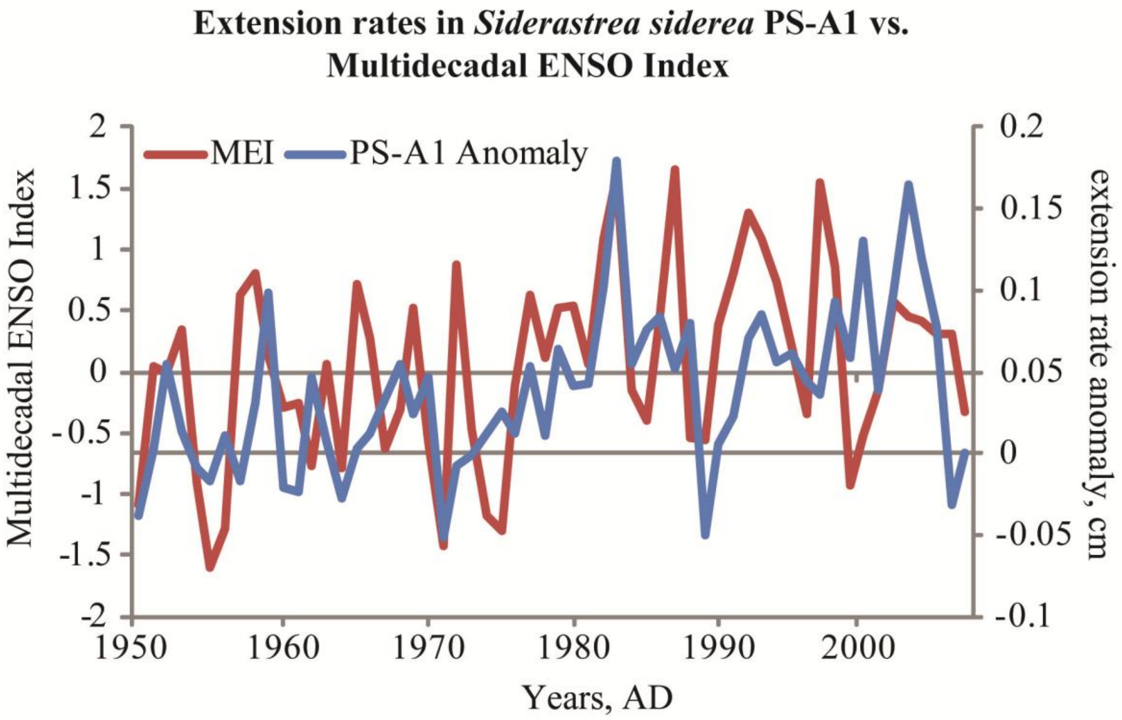

Figure 13. The extension rate anomalies of *S. siderea* correlated significantly with MEI (r=0.43, P=0.0008).

Atlantic Multidecadal Oscillation (AMO) anomaly (http://www.esrl.noaa.gov/psd/data/correlation/amon.us.long.data) was compared to coral extension rate anomalies. AMO is SST variation which affects the climate of Northern Hemisphere (Dijkstra et al., 2006). It is usually accompanied by changes in the rainfall patterns in North America with anomalous SST across Northern Atlantic. The AMO anomaly showed no significant correlation with the extension rates of any core (Table 7) agreeing with the findings by Helmle et al. (2011). Like MEI, the effects of AMO vary locally and include different factors, including SST, rainfall, cloud cover, light availability, and storm activity.

Table 7. Presented are r values for each core compared to Key West sea-level anomaly, Multivariate El Nino Southern Oscillation Index, and Atlantic Multidecadal Oscillation anomaly. The bold numbers represent significant correlation when α = 0.05.

Core	Key West Sea Level Anomaly	MEI	AMO Anomaly
PS-A1	**r=0.73 (df=87, P<0.0001)**	**r=0.43 (df=56, P=0.0008)**	r=0.10 (df=117, P=0.2792)
PS-C1	r=0.20 (df=52, P=0.1372)	r=0.02 (df=52, P=0.8859)	r=-0.06 (df=52, P=0.6665)
MK-A1	r=-0.15 (df=33, P=0.4030)	r=0.03 (df=33, P=0.8642)	r=-0.05 (df=33, P=0.7755)
PS-B3	r=-0.19 (df=87, P=0.0815)	r=0.23 (df=56, P=0.0824)	r=-0.11 (df=117, P=0.2337)
PS-C2	**r=0.32 (df=64, P=0.0091)**	r=0.11 (df=56, P=0.4111)	r=0.04 (df=67, P=0.7442)

CONCLUSION

Although relatively small sample size makes it impossible to generalize our findings our study can give some insights into coral extension rates and their response to the environment. The first major conclusion is that the extension rates were, not only species- specific, as was expected, but also specific to the colony. Coral extension rates were variable even within the slabs of the same core demonstrating that the response to the environmental factors is different for each polyp within the colony. Much larger differences were measured in slabs from different cores and species. Despite the variability some similarities were noticed. The corals of the same species that were not affected by disease showed similar patterns and trends in extension rates while those that were diseased showed no correlation with other corals of the same or different species. Each of the three species responded in a unique way to the environment which suggests that some are more sensitive to certain environmental parameters than others. Fast-growing species *Montastraea faveolata* and *Diploria strigosa* had similar trends in extension rates while they differed from the slow-growing *Siderastrea siderea*. Since not all the species and colonies are affected by the environment equally any efforts to preserve and manage reefs in Florida should take this into account.

Generally, the long cores produced the higher correlations with each other and with the environmental parameters. They also demonstrated the need for a great caution when studying short cores. *Siderastrea siderea* was the most useful species in this study. It not only produced over a 100-year record of extension rates but also produced significant correlation with SST, MEI, and SL. The species definitely merits the attention of future studies in the field of climatology of subtropical oceans. The short cores were much less useful than the long cores and one must be careful when using a short core to study climate. This study suggests that future studies should focus on longer climate records and be cautious when using shot cores.

In order to better protect and manage coral reefs that face great threats from anthropogenic pollution and climate change we need to further our understanding on how corals grow and what environmental factors affect them. Only then we can prioritize and make a management programs for effective protection and management of reef communities and reverse the worldwide declining trend in coral growth.

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