CLIMATE CONTROLS ON CORAL GROWTH IN THE CARIBBEAN

By

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OUTLINE

Abstract

Accurate predictions of Caribbean coral reef responses to global climate change are currently limited by a lack of knowledge of the dominant environmental controls on coral growth. Corals exhibit significant responses to environmental variability occurring on multi-annual to decadal timescales, which are significantly longer than the duration of typical laboratory and field-based experiments. Skeletal growth records, which provide annually-resolved histories spanning several centuries, enable links to be established between coral growth and both long term trends and low-frequency oscillations in environmental conditions. We used 3-D CT scan and imaging techniques to quantify the growth of 3 massive corals (*Siderastrea siderea*) from the US Virgin Islands (USVI) over the period 1950-2009 and compared these growth rates to other records collected from the USVI, Puerto Rico, the Yucatan, Belize and the Bahamas. While coral growth rates were inversely correlated to sea surface temperature (SST) in the Western Caribbean basin (Yucatan, Belize, Bahamas), we found no significant relationship between SST and coral growth in the Eastern basin (USVI, Puerto Rico). Instead, we found a significant inverse relationship between coral growth in the Western Caribbean and changes in the Atlantic Multidecadal Oscillation and a significant positive relationship between coral growth in the Eastern Caribbean Region and shifts in the Pacific Decadal Oscillation. Using data from the Simple Ocean Data Assimilation (SODA) we compared the wind field anomalies during periods of positive coral growth in both regions with the wind field anomalies during phases of these climactic modes that are conducive to coral growth. We find that both the AMO and the PDO play a significant role in shifting the mean wind patters in these Caribbean regions, with the PDO primarily affecting wind patters in the Eastern Basin and the AMO affecting wind patterns in the Western basin. We suggest that the altered wind patterns associated with these modes may induce upwelling favorable conditions in their respective regions of influence, increasing the availability of nutrients for coral growth.

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1. Introduction

1.1 Importance of Coral Reefs

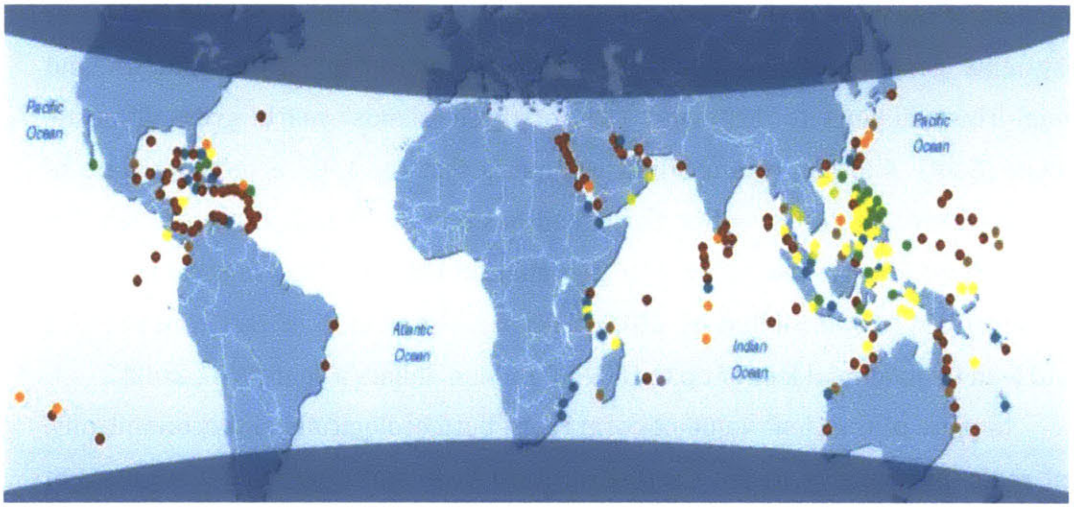

Figure 1. Map of the location of tropical coral reefs. [adapted from Bryant et al. (1998)]

Coral reefs occupy less than 0.0025% of the Earth's marine environment yet they are home to 25% of all marine fish species (Burke et al., 1998). Overall, coral reefs support more species per unit area than any other marine environment: an estimated 4,000 species of fish and 800 species of hard corals alone (Reaka-Kudla, 1997). The biodiversity of reefs is also key to the discovery and development of new drugs. Already medicines for cancer, arthritis, bacterial infections and viruses are being developed from compounds discovered in coral reef animals (Bruckner, 2002; Tacio, 2008). Globally, coral reefs are worth an estimated US$375 billion, providing economic and environmental services, both directly and indirectly, to an estimated 1/10th of the world's human population.

The services coral reefs offer range from direct provisioning services such as food and raw materials, to regulating services such as protection from storm surges and sea level rise, to indirect cultural services such as opportunities for tourism and recreation (TEEB, 2009). Protecting reefs in the Caribbean is particularly important as many of the island nations rely on tourism as their sole source of income and are thus at major economic risk if their reefs collapse (Bryant et al., 1998). A 2006 evaluation of the coral reefs of Trinidad & Tobago and St. Lucia estimated that these ecosystems generate US$94 and US$44 million respectively from tourism and fishing. This amounts to 11% and 15% of these islands' yearly gross-domestic product (GDP). Another recent study estimated that the total economic value of reef-related tourism in the entire Caribbean basin in 2000 amounted to US$4,700 million. Projections assuming no reef degradation estimate that this value would increase to US$13,000 million by 2015, whereas degradation of reef communities would lead to an annual loss of up to US$600 million dollars a year (WRI, 2004).

In spite of the clear value of coral reefs, both ecologically and economically, coral reefs, particularly in the Caribbean, have been suffering from a number of different stressors and are one of the ecosystems at most immediate risk from anthropogenic carbon emissions and climate change.

1.2 Decline of Caribbean Reefs from 1970-2000

The health of Caribbean coral reefs has declined precipitously over the past several decades owing to a multitude of stressors, both natural and anthropogenic (figure 2). In a 2003 study, Gardner et al. conducted a meta-analysis of patterns in Caribbean coral cover and reported that coral reefs have suffered an unprecedented 80% decline in live coral cover over the past two decades. Likewise, further studies from specific reef sites across the Caribbean have indicated a concurrent deterioration in the complexity of reef architecture (Gardner et al. 2003; Hughes 1994; Alvarez-Filip et al. 2011; Buddemeier et al. 2011). Anthropogenic stressors contributing to the decline in coral heath include direct agents such as development, tourism, overfishing and pollution as well as indirect agents associated with global climate change such as increased fluxes of African dust (Shinn et al., 2000) and rising sea surface temperatures (SST). In the Caribbean, SSTs have risen steadily for the past century (Hoegh-Guldberg, 1999) and according to a modeling study by Donner et al. (2007), thermal stress associated with this SST increase was the highest ever recorded between 1984 and 2005. This basin-wide increase in SST has resulted in an increase in the frequency and severity of mass coral bleaching events and coral disease as well as an increase in the frequency and intensity of hurricane activity (Hughes et al. 2003; Hoegh-Guldberg et al. 2007; Burke & Maidens 2004).

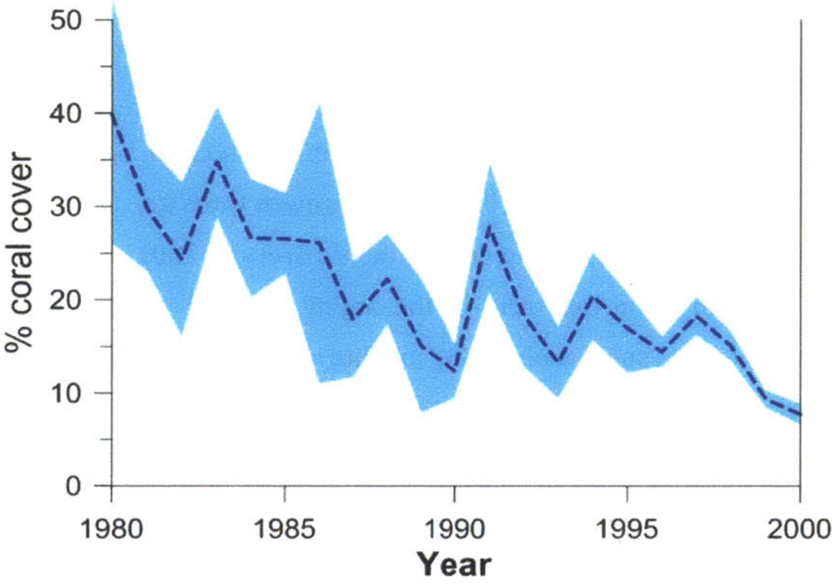

Figure 2. Percent coral cover in the Caribbean [*adapted from Gardner et al., 2003*]

On annual time scales, thermally induced bleaching and disease have been recognized as the major factors responsible for the large decline in live Caribbean coral cover (Bruckner & Hill 2009; Miller et al. 2009) whereas the decline in architectural complexity has largely been associated with an increase in hurricane frequency (Alvarez-Filip et al. 2011). On longer, decadal to centennial time scales, the decline in coral growth has been directly associated with the increasing trend in SST (Saenger et al. 2009; Vasquez-Bedoya et al., 2012). Because, however, each of these drivers varies in scale, both temporally and spatially, there remains much uncertainty as to which are most responsible for the observed decline in coral health over the 20 year period between 1980-2000 (Hughes & Connell 1999; Maina et al. 2011).

1.3 This Study

This study focuses on the long-term effects of climate variability on coral skeletal growth for an extended period from 1950-2010. As coral growth rates are tightly linked to the physical properties of the marine environment (Grottoli, 2001), these background conditions play an important role in the ability of coral species to withstand extreme, episodic events such as bleaching and hurricane activity. To gain a new perspective on the relationship between coral growth and large-scale physical parameters, I conducted two separate but overlapping projects which were designed to address this issue from different angles. The first project involved an in-depth study of the physical oceanography of the Caribbean basin, combining both previously published work with my own analysis of the physical parameters of the Caribbean basin using data from the Simple Ocean Data Assimilation (SODA) v2.2.4. The second project involved analyzing coral growth rates from a suite of sites across the Caribbean basin and Bermuda and comparing these growth rates to available climate records. A final synthesis of the two projects looks at the relationship between the generated growth rate records, Caribbean physical oceanography and large-scale modes of climate variability to determine how these modes might have influenced Caribbean coral growth in the past and to infer how corals might respond in the face of future climate change.

2. Historical Review & Background

2.1 Oceanography and Climate of the Caribbean Basin

2.1.1 Ocean Currents

In the ocean, there are two main processes that control current flow and direction (1) wind stress and (2) changes in water mass temperature and salinity (Stommel, 1957). Because the Caribbean basin lacks extreme variations in temperature and a predominance of evaporation over precipitation, there is insufficient thermohaline convection to drive the currents. Instead, Caribbean currents are driven primarily by the wind, which is dominated by the Northeast trades. Both winds and water flow are seasonal and are strongest in the spring months (Gordon, 1967).

The Caribbean basin is a region of complex bathymetry, comprised of a number of deeper basins punctuated by shallow island passageways (figure 3). Although, the mean surface current in the Caribbean is hard to define due to its incredibly variable nature, it is mainly dominated by the Caribbean current in the southern part of the basin, which is fed by ocean transport through the major island passages. This inflow of water to the Caribbean is distributed nearly equally

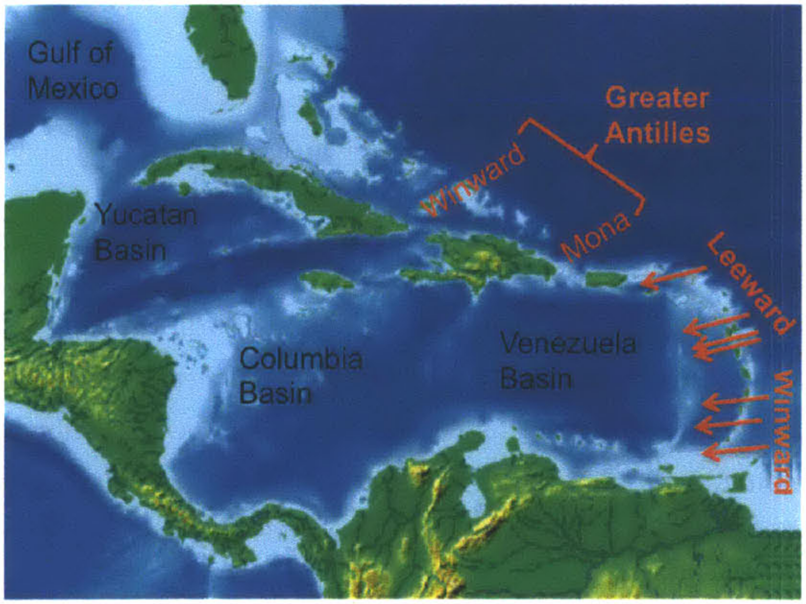

Figure 3. Map depicting the bathymetry of the Caribbean Basin, including the major basins and island passageways.

between the windward island passages (Grenada, St. Vincent, St. Lucia), the leeward island passages (Dominica, Guadeloupe, Antigua, Anegada) and the greater Antilles passages (Mona, Windward) with 10, 8 and 10 Sv of water entering through these passages, respectively (Johns et al., 2002). North of the Yucatan channel, the dominant current becomes the Yucatan current, then the Loop current in the Gulf of Mexico and finally, the Florida current as it exits the Caribbean and enters the Atlantic (Alvera-Azcárate et al., 2009). These Western Boundary surface currents are the strongest in the Caribbean with speeds of greater than 0.8 m/s (Centurioni & Niiler, 2003). Surface currents in the Eastern Caribbean and the Eastern Yucatan basin are dominated primarily by eddy motions. East of the Antilles islands, the flow is mostly Northward in direction and thought to be mainly wind driven (Lee et al., 1996), this current is referred to as the Antilles Current (figure 4).

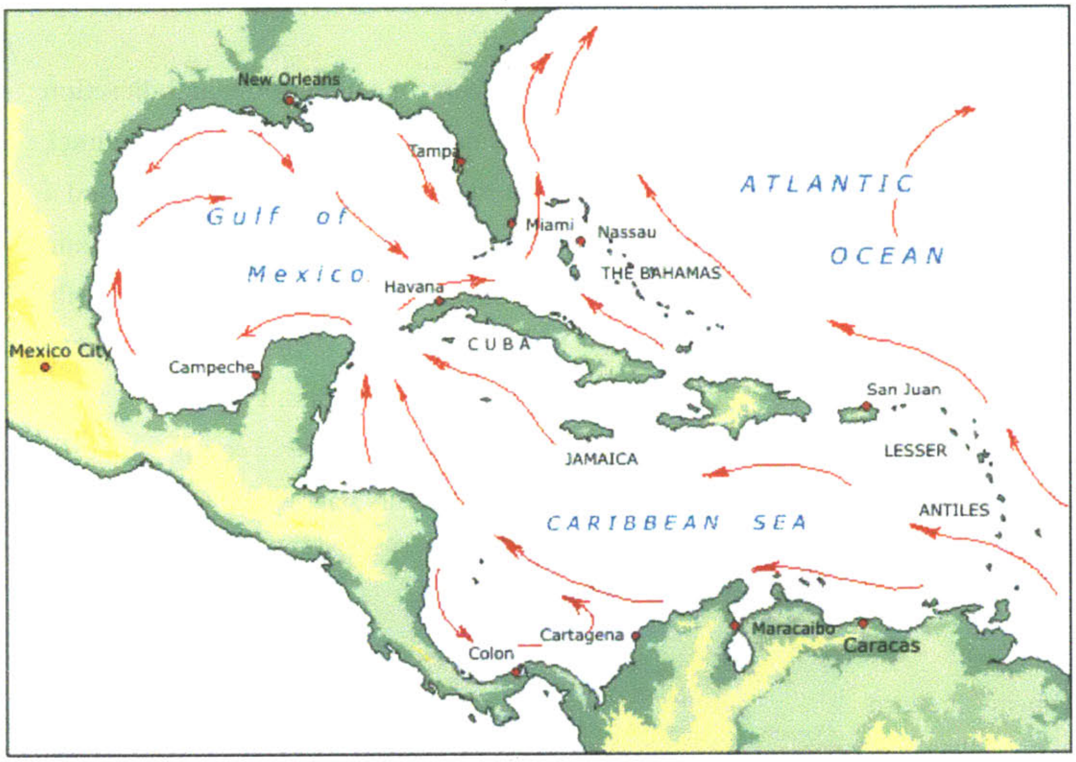

Figure 4. Map of the major Caribbean currents.

The deep circulation of the Caribbean is highly influenced by the deep ocean passageways, the deepest of which are the Anegada Passage between the British Virgin Islands and Anguilla and the Windward Passage between Cuba and Hispaniola with depths of 1900 and 1700m, respectively. Approximately 0.2 Sv of water enters these passages, ventilating the Venezuelan, Columbian, Cayman and Yucatan basins. East of the Antilles islands, a deep western boundary current comprises part of the North Atlantic thermohaline circulation (Lee et al., 1996). The deep central Caribbean circulation is characterized by a cyclonic gyre that transports approximately 15 Sv of water (Joyce et al., 2001; Roemmich, 1981).

2.1.2 Modes of Climate Variability

Climate modes are variations in the climate system with identifiable characteristics, regional patterns and often oscillatory behavior. The most identifiable mode of climate variability is the seasonal cycle, but other modes which are quasi-periodic and less predictable also affect regional climate (Kaplan, 2011). Climate modes are all inherently linked through atmospheric teleconnections and their influence on specific regional climates is often complex as the relative contribution of individual modes can change with time (figure 5). The climate of the Caribbean basin is primarily influenced by 4 different modes of climate variability: the Atlantic Multidecadal Oscillation, the North Atlantic Oscillation, the El Nino-Southern Oscillation and the Pacific Decadal Oscillation. Each of these modes operates on different time scales and influence the climate through interactions between the troposphere, stratosphere, the ocean, adjacent land masses, the pole-equatorial gradient and remote forcing from the Pacific (Marshall et al., 2001).

The North Atlantic Oscillation (NAO) is one of the dominant modes of climate variability in the Atlantic and is most pronounced during Northern Hemisphere winter. It reflects a gradient in sea level pressure (SLP) between the Atlantic subtropical high and the polar low and can be calculated as either the SLP difference between Reykjavik, Iceland and Lisbon, Portugal, using station data, or as the

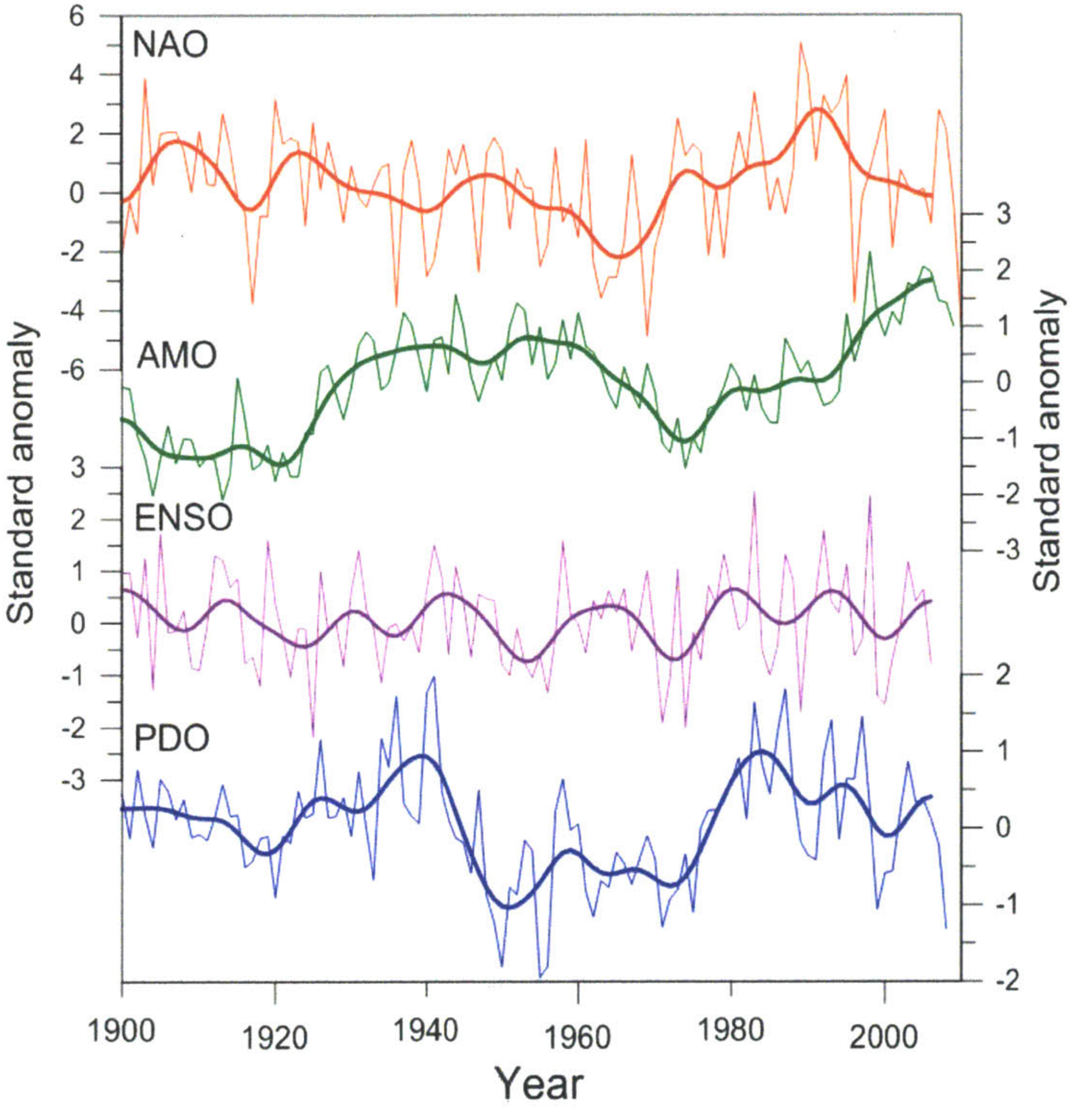

Figure 5. A time series of the different modes of climate variability affecting the Caribbean basin. Thin colored lines represent the annual variation, thick colored lines represent a 10-year Gaussian filter.

principle empirical orthogonal function of surface pressure in the North Atlantic (Hurrell and Deser, 2009). The NAO oscillates between a positive and negative phase every couple of years. When the NAO is in its positive phase the pressure gradient induces stronger westerly winds across the mid-latitudes, bringing colder and drier conditions over the NW Atlantic and Mediterranean regions and warmer and wetter conditions in the eastern United States, northern Europe and parts of Scandinavia (Visbeck et al., 2001). In the negative phase the storm track is weaker and more eastward in direction, resulting in wetter winters in Southern Europe and the Mediterranean and a colder Northern Europe.

The Atlantic Multidecadal Oscillation (AMO) is the leading mode of Atlantic SST variability on decadal time scales. It is calculated by averaging SSTs in the Atlantic Ocean and removing the long-term trend to minimize the influence of greenhouse gas induced global warming (Trenberth and Shea, 2005). The AMO oscillates between periods of anomalously warm SST and periods of anomalously cool SST with a periodicity of about 50-90 years (Enfield et al., 2001). It is thought that variations in the AMO may be linked to changes in Atlantic meridional overturning circulation. The AMO has a large influence on Northern Hemisphere climate and is correlated to air temperature and rainfall over much of the Northern Hemisphere (Sutton and Hodson, 2005). Atlantic hurricanes (Goldenberg et al., 2001) and Sahel droughts (Zhang and Delworth, 2006) are also thought to be linked to AMO variability.

Pacific modes of climate variability, such as the El Nino-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO), also influence Caribbean climate through atmospheric teleconnections (Taylor et al., 2002). ENSO is a strongly coupled mode of tropical ocean-atmospheric variability. The Southern-Oscillation is an inter-annual fluctuation of atmospheric pressure over the tropical Indo-Pacific region and is typically defined as the different in sea level pressure between Tahiti and Darwin, Australia. Negative values of the Southern Oscillation Index, when SLP is high in the Western Pacific, correspond to El Niño episodes which are periods of anomalously high SSTs in the Central and Eastern Pacific. Conversely, positive SOI values correspond to low SLP in the Western pacific and La Niña events when SSTs in the central and Eastern Pacific are anomalously cool (Trenberth et al., 2007). During an El Niño event, there is a weakening of the Easterly trade winds which would normally keep warmer water in the west of the Pacific basin. Instead, anomalously warm temperatures occur eastward causing the thermocline to deepen and impeding upwelling in the Eastern Pacific. Instead, the weakened easterly wind and the relaxed thermocline impede upwelling in the Eastern Pacific, causing the anomalously warm temperatures to extend eastward. La Niña is characterized by increased trade winds, a deeper thermocline, increased upwelling in the eastern Pacific and a more westerly warm pool. ENSO occurs with a periodicity of approximately 2-7 years and is thought to be largely driven by feedback mechanisms involving changes in sea surface temperature gradients and sea level pressure across the pacific (Bjerknes, 1969).

The Pacific decadal oscillation (PDO) is a long-lived El Niño-like pattern of climate variability in the Pacific and has links to ENSO but operates on longer 20-30 year time scales (Mantua and Hare, 2002). It is defined as the leading empirical orthogonal function of Pacific sea surface temperature north of 20°N (Schneider & Cornuelle, 2005). The PDO is thought to be forced by several different mechanisms including (1) remote forcing by ENSO (Newman et al., 2003), (2) atmospheric forcing associated with fluctuations in the position and strength of the Aleutian low, (3) ocean circulation anomalies in the Kuroshio-Oyashio Extension region (Schneider & Cornuelle, 2005).

Modes of climate variability influence Caribbean climate either directly through changes in SST (Enfield, 1996, Enfield and Alfaro, 1999, Spence, 2004) and/or indirectly through atmospheric teleconnections. One of the primary controls on Caribbean climate is the Caribbean Low Level Jet (CLLJ) which has a strong influence on Caribbean precipitation. The CLLJ, defined as the maximum easterly zonal wind at 925 hPA, is a dominant feature of Caribbean summer climate and is associated with precipitation anomalies and tropical cyclogenisis (Wang, 2007). The CLLJ varies sub-annually with two maxima, one occurring in the summer and one occurring in the winter and two minima, one in the fall and one in the spring. The summer maxima is associated with maximum SLP and a minimum of rainfall and cyclogenisis. Variations in the CLLJ are influenced by Caribbean SLP which is in turn influenced by variations in the North Atlantic Subtropical High (Wang, 2007).

The CLLJ can be alternately forced by either the AMO or ENSO and varies synchronously with the NAO. There is a strong relationship between the NAO and the CLLJ since a strong North Atlantic subtropical high is associated with both a positive NAO and an intensification of the CLLJ. When the CLLJ is forced by the AMO there is a uniform intensification of wind across the jet. A positive AMO increases Caribbean convection and promotes the formation of easterly tropical waves (atmospheric troughs of low pressure) which bring increased rainfall over much of the Caribbean during the early rainy season (May-July; Taylor et al., 2002). ENSO affects the CLLJ through its influence on the North Atlantic Subtropical High which is opposite during the summer and winter months. This means that during the winter, warm SST anomalies in the Pacific (ie. El Nino) correspond to a weakened CLLJ, conversely, during the summer, El Niño years correspond to a strengthened CLLJ (Wang, 2007). The opposite is true for La Niña years. ENSO predominantly influences the Caribbean's late rainy season (August-October), with El Niño years resulting in a milder late season and La Niña resulting in a wetter late season (Taylor et al., 2002).

Caribbean SST, rainfall and wind strength are all tightly linked to variability in the climate modes which have an impact on local air-sea feedback. Marshall et al. (2001) propose that tropical Atlantic variability is jointly forced by changes in the NAO and ENSO and their influence on SST and wind strength anomalies. The NAO remotely forces tropical SSTs, as does ENSO, possibly through a reduction in surface latent heat flux associated with a reduction in trade wind strength (Klein et al., 1999). The joint influence of these two modes can act to warm tropical SSTs and lower sea level pressure resulting in a weakening of the northeast trade winds and a strengthening of the southeast trades (Marshall et al., 2001).

2.2 Coral Growth Records

2.2.1 Coral Growth

Tropical reef-building corals grow their calcium carbonate skeletons in annual bands of alternating high and low density layers. Knutson et al. (1972) first recognized the potential use of these bands for the recovery of information on coral growth histories and proxy reconstructions of environmental records. Three growth parameters can be assessed from coral skeletons, namely annual extension rate, average annual density and coral calcification rate, which is a product of the annual average density and the annual extension rate. Although, Dodge and Brass (1984) suggest that all three parameters are necessary to obtain a coherent understanding of the link between coral growth and environmental parameters, several recent studies have shown that coral extension rates alone can reflect the coral's response to environmental stress (Cantin et al., 2010; Copper et al. 2008; De'Ath et al., 2009).

Three main growth processes occur during skeletal formation: (1) the addition of new skeleton at the outer surface of the coral colony (2) the thickening of the existing skeleton, which occurs throughout the depth of the tissue layer, and (3) the periodic and rapid uplift of the lower margin of the tissue layer associated with the formation of new skeleton (Barnes and Lough, 1993). The interplay between these three processes governs the formation of either a high density band or a low density band. While it is still unclear exactly when corals secrete their high and low density bands, Highsmith (1979) suggests that for three different species of massive coral in the Pacific (*Favia pallida, Goniastrea retiformis, Porites lutea)* and in the Caribbean (*Montastrea annularis, Montastrea cavernosa, Porites astreoides*), high density bands are formed during periods of seasonally higher SST and less light availability, whereas low density bands are formed during periods of seasonally lower SST and higher light availability. In the Caribbean, this implies that high density bands for *M. annularis* and *M. faveolata* are typically formed during the months of July and September when SSTs are highest (Carricart-Ganivet et al., 2001;

Cruz- Piñón et al., 2003). Other factors such as coral reproductive cycles, nutrient availability, turbidity, sedimentation and wind stress have also been invoked as contributing factors to density band formation, and as a result, overall annual coral skeletal extension (Barnes and Lough, 1993).

Hudson (1981) describes three major factors governing growth of *Montastrea annularis* in Florida, namely, water depth, turbidity and temperature. Several studies have since confirmed the relationship between linear extension and water depth, with corals generally growing faster in shallow reef environments than in off shore reef environments (Cruz-Piñón et al., 2003; Dodge & Brass 1984; Carricart-Ganivet & Merino 2001).

Previous studies have also suggested that there is a fundamental dependency of coral growth rates on temperature (Marshall & Clode, 2004; Coles, 1978, Jokiel and Coles, 1977; Clausen and Roth, 1975). The three inter-related growth parameters, namely calcification, skeletal extension and density, are all thought to be controlled by two main factors: (1) the energy available for active deposition of calcium carbonate and (2) the means by which the calcium carbonate is used to construct the skeleton. Different growth strategies are linked to the latter factor, with corals choosing to invest their calcium carbonate either in linear extension or in skeletal density (Carricart-Ganivet 2004; Carricart-Ganivet 2007). Growth strategies have been shown to vary across a variety of species in different Caribbean locations in response to SST (Elizalde-Rendon et al., 2010, Carricart-Ganivet 2004,2007; Davalos-Delhullu et al., 2008). In individual coral colonies calcification rate is generally linked to skeletal growth, so that these two parameters vary synchronously with changes in temperature. This means that an assessment of coral skeletal extension rate alone can often give valuable information on the environment in which corals have grown.

Studies in the field show that both light and temperature exert an important effect on skeletal growth but are unable to distinguish between the effects of these two environmental parameters (Yap and Gomez, 1984). Both short-term laboratory studies measuring ^{45}Ca incorporation (Clausen and Roth, 1975; Marshall and Clode, 2004) and long-term laboratory studies measuring changes in skeletal weight (Coles and Jokiel, 1978; Jokiel and Coles, 1977) have demonstrated that coral growth peaks within a narrow range of optimal temperatures. For some species of corals in the tropical Pacific, this occurs at seawater temperatures between 25-27°C. Mashall & Clode (2004), however, suggest that this temperature range may vary with latitude and mean annual sea surface temperature. Several studies support this interpretation. An investigation of the growth of *Pocillopora damicornis* from two disparate regions in the Pacific revealed growth peaks at two distinct temperatures: 27°C for corals from Kaneohe Bay, Hawaii where temperatures range from 23-27°C and 31°C for corals from Enewetok Atoll, Western Pacific, where mean SSTs are 2-3°C higher (Coles et al., 1976; Clausen & Roth, 1975).

Reef ecosystem studies have shown that coral skeletal growth is an essential factor in the resilience of a reef to environmental stressors (Hoegh-Guldberg et al., 2007) where "resilience" is defined as the rate at which an ecosystem returns to a given state after a perturbation or disturbance (e.g. bleaching) (Hughes et al., 2003). In fact, Roff & Mumby, (2012) attribute the recent decline in Caribbean coral resilience in part to the loss of fast growing coral in this region. They hypothesize that high individual coral growth rates not only have the potential to increase a population's recovery rate, but that they provide a competitive advantage over algal growth. One of the concerns associated with the Caribbean-wide decrease in coral cover is that the Caribbean may be nearing a "tipping point" where a phase shift would occur from the current, coral-dominated state to an algal dominated state. Once this phase shift has occurred, a new equilibrium would be established with its own resilience and stability making it increasingly hard for the ecosystem to return to a coral dominated state (Mumby et al., 2007; Hoegh-Guldberg et al., 2007). Coral growth rates play an important role in this balance, raising the threshold for a shift between these two phases (Hoegh-Guldberg et al., 2007).

2.2.2. Long-term records of coral growth

(a) Global growth records

On long (>25 year) time scales, temperature has been shown to have an important influence on coral growth in multiple different species located in numerous tropical coral reef locations across the globe. The direct response of the different growth parameters (linear extension, density and calcification), however, varies from place to place. Until relatively recently, the consensus was that coral growth rates would respond positively to rising SST (Lough and Cooper, 2011) and indeed, the majority of studies report coral growth varying directly with SST in *Porites* spp., *Diploria* spp., *M. annularis* and *Pavona spp.* (Dodge, 1981; Hudson, 1981; Hudson and Robbin, 1981; Dodge and Lang, 1983; Glynn and Wellington, 1983; Hudon, 1985; Dunbar et al., 1994; Lough and Barnes, 1997; Nie et al., 1997; Ramsay and Cohen, 1997; Lough and Barnes, 2000; Bessat and Buigues, 2001). This picture has been complicated by a number of studies that have found either a prolonged inverse relationship between temperature and coral growth or a recent shift towards declining coral growth associated with rising SSTs (Dodge and Vaisnys, 1975; Castillo et al., 2011; Saenger et al., 2009; Cantin et al., 2010; Vasquez-Bedoya et al., 2012).

For the most part, corals in the Pacific have exhibited long-lasting positive relationships with SST (table 1). Two studies from the Galapagos found linear extension rates of Pavona sp. to be positively correlated to SST with corals growing most during periods of El Niño warming (Glynn and Wellington, 1983; Dunbar et al., 1994). At Enewetok atoll and in Moorea, French Polynesia extention rates of Porites spp. were also positively correlated with SST and air temperature, respectively. In contrast, Manzello et al. (2010) found that linear extension rates of *Pocillopora damicornis* on the Pacific side of Panama have decreased in concert with rising SSTs since the 1970s.

Table 1. Global coral growth rate sand their relationship to sea surface temperature

Location	Species	Growth parameter	Time period	Relationship to SST	Reference
Galapagos	*Pavona* spp.	linear extension	1585-1953	positive	Dunbar et al. 1994, Glynn and Wellington, 1983
Enewetok Atoll	*Porites lutea*	linear extension	1872-1983	positive	Lough and Cooper, 2011
Moorea, French Polynesia	*Pavona* spp.	calcification, density	1958-1990	positive	Bessat and Buigues, 2001
Panama (Pacific side)	*Pocillopora damicornis*	linear extension	1970, 2006	Growth decreasing	Manzello et al., 2010
South China Sea	*Porites lutea*	linear extension	1961-1993	positive	Nie et al., 1997
Phuket, Thailand	*Porites lutea*	linear extension	1984-1986, 2003-2005	inverse	Tanzil et al., 2009
Great Barrier Reef	*Porites*	calcification, extension	1906-1982	positive	Lough and Barnes, 1997
Great Barrier Reef	*Porites*	calcification, extension	1880-1929, 1930-1979	positive	Lough and Barnes, 2000
Great Barrier Reef	*Porites*	calcification	1988-2003	inverse	Cooper et al., 2008
Great Barrier Reef	*Porites*	calcification	1990-2009	inverse	De'ath et al., 2009
Red Sea	*Diploria heliopora*	extension	1930-2008	inverse	Cantin et al., 2010

Table 2. Caribbean coral growth rate sand their relationship to sea surface temperature

Location	Species	Growth parameter	Time period	Relationship to SST	Reference
East Flower Garden Banks	*Montastrea Annularis*	growth	1950-1979	positive	Dodge and Lang, 1983
Florida Keys	*Montastrea faveolata*	growth	1937-1996	suggested inverse	Helmle et al., 2011
Belize	*Siderastrea siderea*	linear extension	1930-2000	inverse	Castillo et al., 2011, Castillo et al., 2012
Belize	*Siderastrea siderea*	linear extension	1936-2001	inverse	Saenger et al., 2009
Yucatan	*Siderastrea siderea*	linear extension	1860-2008	inverse	Vasquez-Bedoya et al., 2012
Bahamas	*Siderastrea siderea*	linear extension	1857-1991	inverse	Saenger et al., 2009
Panama (Caribbean side)	*Siderastrea siderea*	linear extension	1880-1990	no relationship	Guzman et al., 2008
Panama (Caribbean side)	*Acropora palmata*	growth	1971-1973, 2002-2004	suggested inverse	Bak et al., 2009
Bermuda	*Diploria* spp.	growth		inverse	Dodge and Vaisnys, 1975
Visques, Puerto Rico	*Montastrea Annularis*	growth	1946-1970	positive	Dodge (1981)

In the South China Sea, linear extension rates of 5 samples of *Porites lutea* collected from the Xisha Islands and Southern Hainan Island were positively correlated to SST from 1961-1993 (Nie et al., 1997). Growth rates of *Porites lutea*, however, collected from 8 different sites in Phuket, Southern Thailand during 2 distinct time periods (1984-1986 and 2003-2005) have declined while temperatures have risen. The authors suggest that corals in this area have been exposed to temperatures beyond their thermal maximum resulting in the observed inverse relationship between SST and coral growth (Tanzil et al., 2009).

Numerous studies have looked at long-term coral growth rates of *Porites* spp. from the Great Barrier Reef (GBR). Early studies examining growth rates of numerous coral colonies across the GBR, pre-1980 find consistent positive relationships between coral growth and SST. More recent studies, however, show a different trend. Cooper et al. (2008) found a 21% decrease in coral calcification rates from 1988-2003 in two different *Porites* populations located 450km apart on the northern GBR. Another recent study by De'ath et al. (2009) examining the growth rates of 328 colonies of *Porites* spp. from 69 reefs across the GBR found similar decreases in calcification and extension since 1990. Both stdies attribute this decline to a combination of rising SSTs (and associated thermal stress) and declining saturation states of seawater aragonite.

Growth rates in the Red Sea have also shown unprecedented declines in recent years (Cantin et al., 2010). Growth of the dominant massive species *Diploria heliopora* was shown to be inversely correlated to summer SST over the 70 year time period from 1930-2008. Cantin et al. (2010) attribute the inverse relationship between coral growth and temperature to a decrease in the photosynthetic capacity of symbiotic zooxanthellae with increasing temperatures but do not account for the consistency of the inverse relationship between coral growth rate and temperature over the entirety of the record.

(b) Caribbean growth records

Coral growth rates in the Caribbean are much more spatially variable than other tropical basins with an emerging geographical trend in the relationship between coral growth and SST (table 1). As I will show, coral sites located along the Caribbean current all seem to have an inverse relationship with SST, whereas corals located elsewhere in the Caribbean and Gulf of Mexico appear to have the predicted positive relationship between coral growth and SST.

In the Gulf of Mexico, Dodge and Lang (1983) found a positive correlation between the growth of 12 specimens of *Montastrea annularis* (data originally from Hudson and Robbin, 1981) and SST in reefs on the East Flower Gardens Bank (Northwest Gulf of Mexico) for the period 1950-1979. The same corals were then reanalyzed by Slowey and Crowley (1995), who used a 9-point Gaussian filter, to reveal a decline in coral growth rates in the late 1950's coincident with a major shift towards colder winters.

Helmle et al. (2011) reported a small, but significant increase in the growth of 7 specimens of *M. faveolata* from the Florida Keys over the period 1937-1996. Although there is not a significant relationship between coral growth and SST, SSTs in this area decreased during this period, suggesting that, were growth rates and SST correlated, there would be an inverse relationship between coral growth and SST. The data may instead suggest that growth rates of *M. faveolata* from the Florida Keys are not driven primarily by temperature variations.

Numerous coral growth studies have been conducted in the Western Caribbean, most of which find that coral growth rates are decreasing in concert with rising SSTs over the past several decades (Guzman et al. 2008, Manzelo et al., 2010, Castillo et al., 2011, Castillo et al., 2012, Vasquez-Bedoya et al., 2012). In Belize, fore-reef colonies of *Siderastrea siderea* showed a significant decrease in linear extension from 1930-2000, whereas linear extension in colonies on the near shore and back reef showed almost no change (Castillo et al., 2011, Castillo et al., 2012).

The authors, therefore, suggest that fore-reef colonies are likely to be most susceptible to the changing environment.

In the Yucatan, Vásquez-Bedoya et al., (*in press*) found a significant, inverse relationship between coral growth rates and SST, and between annual linear extension and the Atlantic Multidecadal Oscillation (AMO) – the leading mode of SST variability in the North Atlantic – for the period 1860-2008. This relationship is consistent with the findings of Saenger et al. (2009) who reported a significant, inverse relationship between coral growth rates of *Siderastrea siderea* and SST for single corals from Belize and the Bahamas over the entire length of overlap with the instrumental record (1936-2001 and 1857-1991, respectively).

Using corals from the eastern coast of Panama, Guzman et al. (2008) constructed a master chronology of coral growth using 77 cores of *Siderastrea sidera* and found that coral growth declined over the period 1880-1990. They found no relationship, however, between coral growth and SST, but instead attributed this decline in coral growth to an increase in runoff and sedimentation associated with the construction of the Panama Canal. Likewise, Bak et al. (2009) found that growth of *Acropora palmata* decreased by 7% in the winter and 11% in the summer between the periods 1971-1973 and 2002-2004.

Dodge and Vaisnys (1975) found a consistent inverse relationship between coral growth rates in Bermuda and air temperature using an index constructed with 27 specimens of *Diploria* spp.. They attributed this inverse relationship to a positive relationship between coral growth rates and nutrients (and an inverse relationship between nutrients and temperature).

Studies from the Eastern Caribbean, near the Antilles region, suggest that, unlike in the region of the Caribbean current, the relationship between coral growth rates and SST is predominantly positive. Using a combination of multiple corals of *M. annularis* from the island of Visques, Puerto Rico, Dodge (1981) found a positive correlation between coral linear extension and water temperature over the 20 year period from 1946-1970.

It is clear from the discrepancy between these growth rate studies and their relationship to SST, especially in the Caribbean, that there remains a gap in our scientific understanding of the dominant environmental controls on coral growth. This study aims to elucidate our understanding of the relationship between environmental parameters and coral growth by providing perspective on the potential role of large-scale modes of climate variability on annual skeletal extension rates.

3. Methods

3.1 Coral collection and preparation

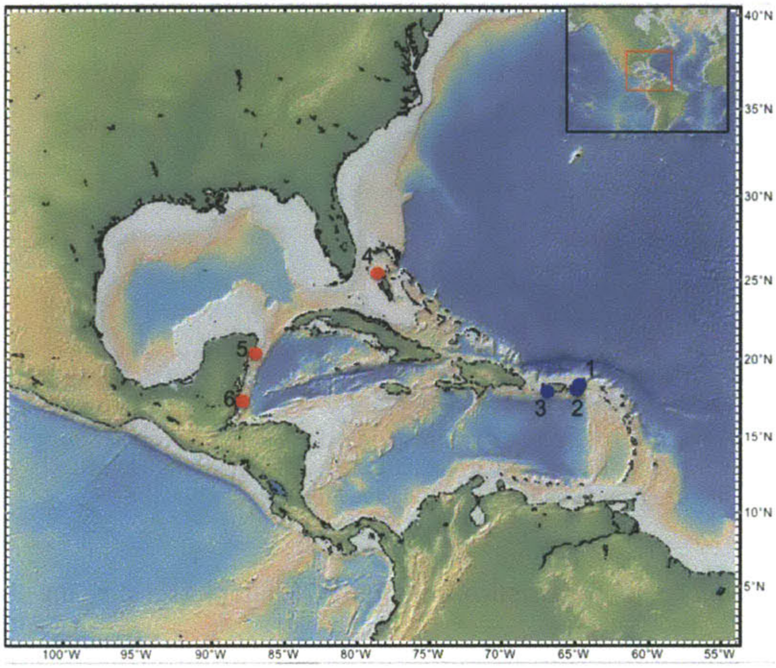

Figure 6. Map showing coral reef locations where samples were collected (see table 1 for site references). Red (green) dots were used to construct the West (East) Caribbean compilation record.

Coral cores were collected in October, 2009 from live colonies of the dominant massive coral *Siderastrea siderea* from two sites in northern St Thomas, near Hans Lolik island (18°24.265 N, 64°54.311 W; 18°24.179 N, 64°54.201 W) and from Fish Bay, St. John (figure 6). Additional coral records from Belize, the Yucatan, Bahamas and Puerto Rico were compiled from existing literature (figure 6; table 2).

In the lab, cores were scanned to reveal annual density bands, using a Siemens Zoom Computer Assisted Tomography (CAT) scanner at the Woods Hole Oceanographic Institution using CT-scan methods outlined in Cantin et al. (2010). 3-D computerized imaging techniques (OSIRIX) were used to accurately identify the axis of maximum vertical growth and to slice the 3D image to an optimal thickness revealing the annual high and low density band couplets. CT-scanning is advantageous as it allows for unlimited attempts to determine the axis with the

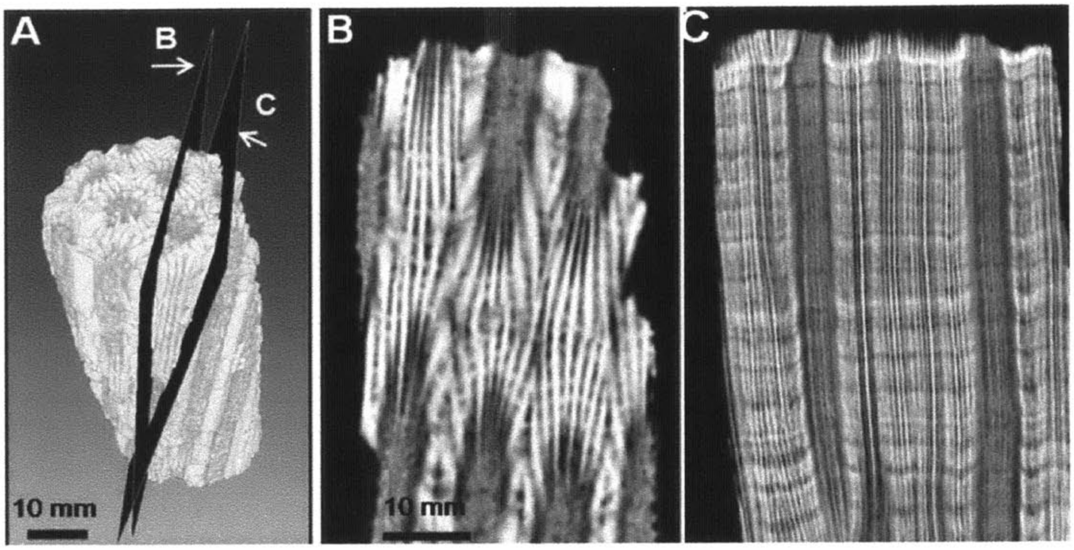

Figure 7. Quantification of annual coral growth by 3D CT scanning. (**A**) 3D CT scan reconstruction of the skeleton. (**B**) A slice cut subparallel to the upward growth axis (**C**) A slice cut parallel to the upward growth axis, reveals clear annual growth bands. [*adapted from Cantin et al., 2010*]

clearest bands. Figure 7(b), depicts an off-axis slice, and figure 7(c) depicts a slice on axis with the clear banding pattern.

On the 2-D slice, density profiles were constructed down the entire length of each core. The distance between successive high-density bands was used to calculate the annual upward extension of each coral. Although some cores extended back to the 18th and 17th century, we chose to focus on the period 1950-2009 to allow for the maximum overlap between cores.

In order to do a quantitative comparison of calcification rate and linear extension over a short portion of our cores, I calculated calcification rates in the following way. Average annual skeletal densities (in grams per cubic millimeter) were quantified from the CT images of each core by converting grayscale values to apparent absolute density using hydroxyapatite standards of known density (Cantin et al. 2010 SOM). Average annual calcification was then calculated as the product of annual linear extension and annual density.

Table 2. Locations and references for individual coral samples.

Site #	Location	ID	GPS Coordinates	Year	Species	Reference
1	USVI	Hans 11	18°24.265 N, 64°54.311 W	2009	*Siderastrea siderea*	This paper
1	USVI	Hans 12	18°24.179 N, 64°54.201 W	2009	*Siderastrea siderea*	This paper
1	USVI	FISH	18°18.957 N, 64°46.156 W	2009	*Siderastrea siderea*	This paper
2	USVI	ST-COL	18°11.140 N, 65°4.606 W	2008	*Siderastrea siderea*	Tyler Smith
2	USVI	ST-TIG	18°11.330 N, 64°57.395 W	2008	*Siderastrea siderea*	Tyler Smith
2	USVI	ST-SAV	18°20.438 N, 65°4.923 W	2009	*Siderastrea siderea*	Tyler Smith
3	Puerto Rico	KIL	17°55.800 N, 67°00.000 W	2004	*Montastrea faveolata*	Kilbourne et al., 2008
4	Bahamas	BAH	25°50.400 N, 78°37.200 W	1991	*Siderastrea siderea*	Saenger et al., 2009
5	Yucatan	YUC	20°34. 450 N, 87°07. 050 W	2009	*Siderastrea siderea*	Vasquez-Bedoya et al., 2012
6	Belize	BEL	17°30.000 N, 87°45.600W	2001	*Siderastrea siderea*	Saenger et al., 2009

3.2 Regional Coral Chronologies

3.2.1 Construction of the Chronologies

Master index chronologies were constructed for (1) the entire Caribbean and Bermuda, (2) the Western Caribbean and (3) the Eastern Caribbean in order to expose the common trend in coral growth in each of these areas. To construct the index chronologies, raw growth data for each colony were converted to standard anomalies by subtracting yearly growth increments by the overall time series average and dividing by the standard deviation calculated over the same period (Dodge and Lang, 1983; Fritts, 1976).

$$Standard\ anomaly = \frac{extention\ rate - mean}{standard\ deviation}$$

Because each individual record varied in length it was necessary to choose a mean that covered either the entirety of the individual records (EM) as in Dodge and Lange (1983), in which case the mean was different for each record, or a mean that was common to all records (Entire Caribbean Chronology: 1985-1991, Western Caribbean: 1950-1991, Eastern Caribbean: 1985-2004) with the largest period of overlap. Both methods were employed to calculate separate East and West growth chronologies and an entire Caribbean chronology. In each case, it was found that there was not a statistically significant difference between the two methods (figure 8). As a result, in order to be consistent we chose to use only the chronologies calculated using the mean calculated over the overlap period for all subsequent analyses.

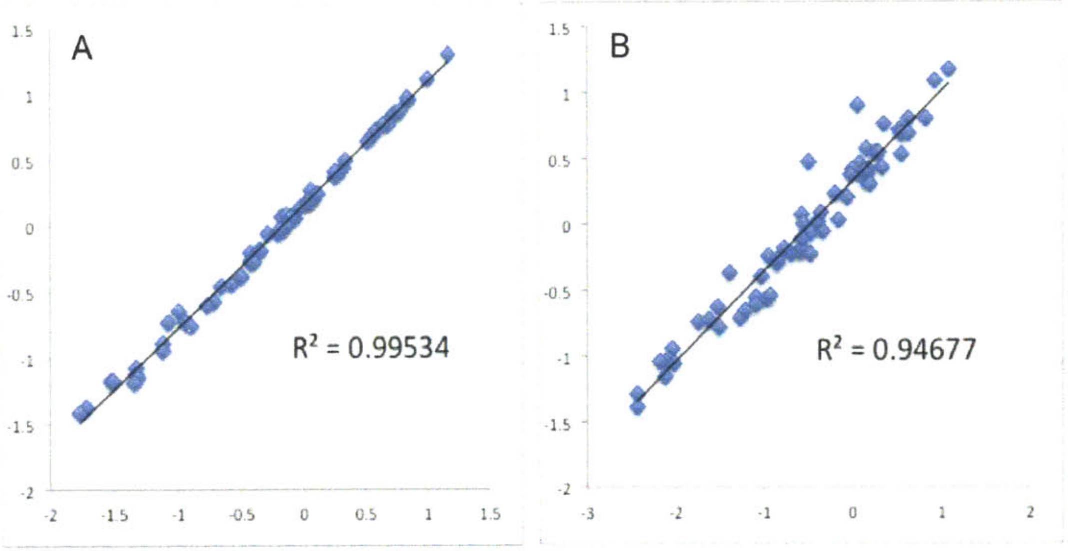

Figure 8. Correlations between the two compilation constructions using either the mean and standard deviation over the entire length of the individual records or over the period of greatest overlap between records for (A) the Western Caribbean and (B) the Eastern Caribbean.

(a) East Caribbean

The East Caribbean chronology was calculated using 5 different corals collected from the Eastern Caribbean islands of Puerto Rico and the United States Virgin

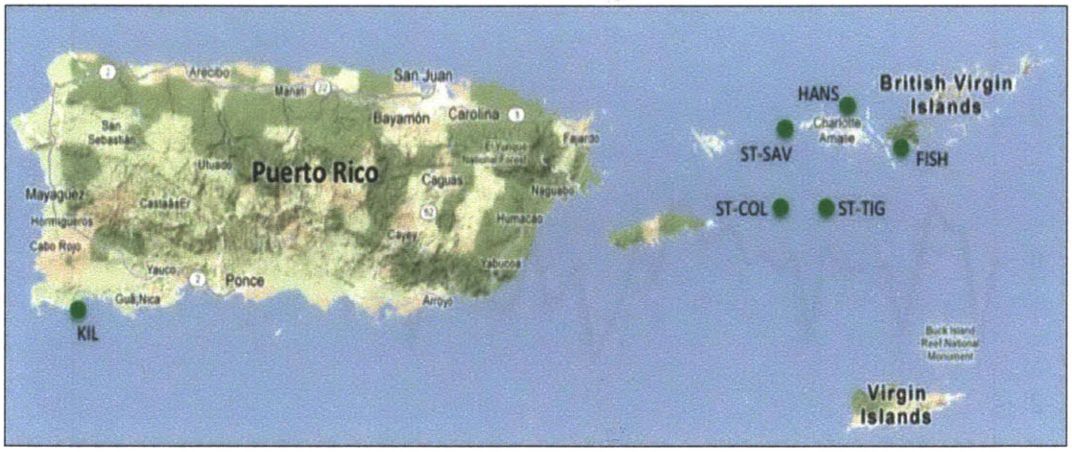

Figure 9. Location of core sites in the Eastern Caribbean. HANS is the only location located on the Northern site of the island.

Islands (USVI) (figures 9,11). The majority of these cores were collected from the southern sides of the islands with the exception of the Hans-Lolik cores (Hans 11, Hans 12), which were collected on the northern side of St. Thomas, USVI.

To construct the master chronology for the East Caribbean, the annual growth rate anomalies calculated for corals from individual site locations were averaged first; this included Hans 12 and Hans 11 to form a Hans average compilation (figure 10) and the corals collected from south of St Thomas (ST-SAV, ST-COL,ST-TIG) to form a ST-average compilation. All annual growth rate anomalies from individual corals (FISH, KIL) and coral site compilations (ST-average) collected from the southern sides of the islands were then averaged to form the East Caribbean compilation (figure 11). The Hans coral compilation was kept separate as it showed different trends from the corals on the southern side of the island (figures 10,11; table 3) leading us to believe that these corals were exposed to a different environmental regime. For the most part, all corals collected on the southern side of the island, however, showed similar trends for the period 1950-2009.

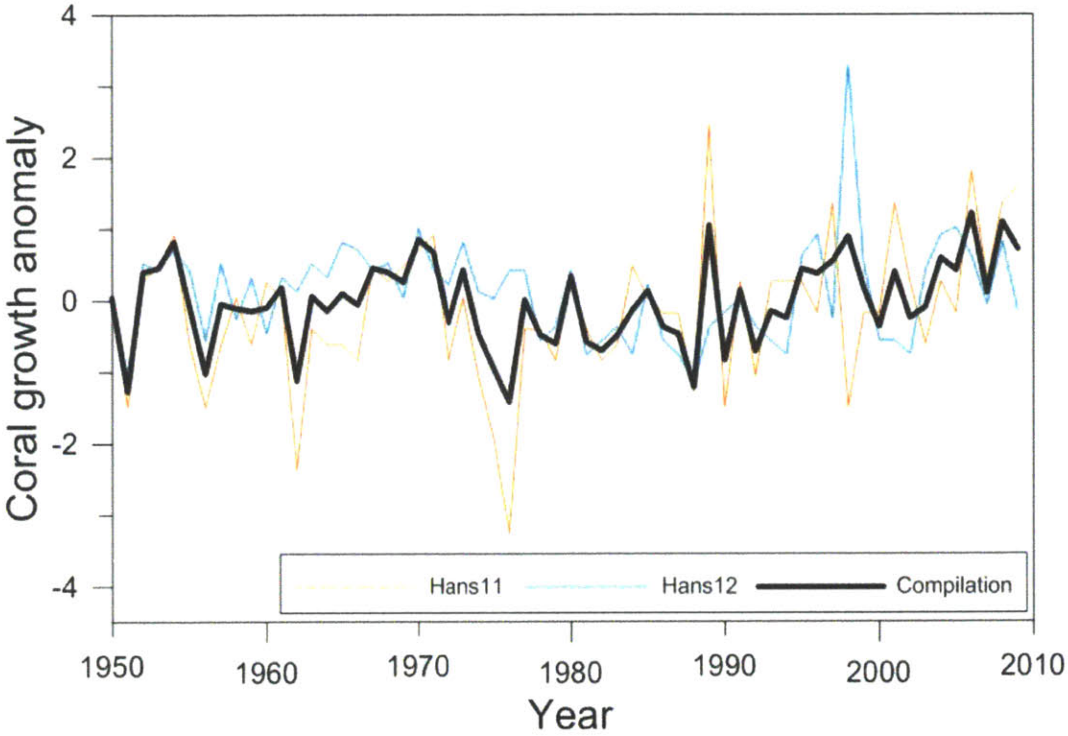

Figure 10. Plot of the individual coral records from the Hans-Lolik site in the USVI (thin colored lines) and the average of these sites (thick black line).

Table 3. Correlation coefficients between coral time series from the Eastern Caribbean over the period of greatest overlap between individual records and between the coral time series and the East Caribbean master chronology index over the period 1985-2004.

Coral ID	H11	H12	FISH	KIL	COL	SAV	TIG
H11	-						
H12	0.11	-					
FISH	0.0628	-0.36	-				
KIL	5.30E-08	-0.128	0.052	-			
COL	0.02144	-0.3	0.2385	0.045	-		
SAV	-0.282	-0.4	0.259	0.243	0.1375	-	
TIG	0.1	-0.14	0.198	0.140	0.088	0.0828	-
East Caribbean Index	N/A	N/A	**0.572**	**0.685**	**0.677**	**0.339**	**0.02258**

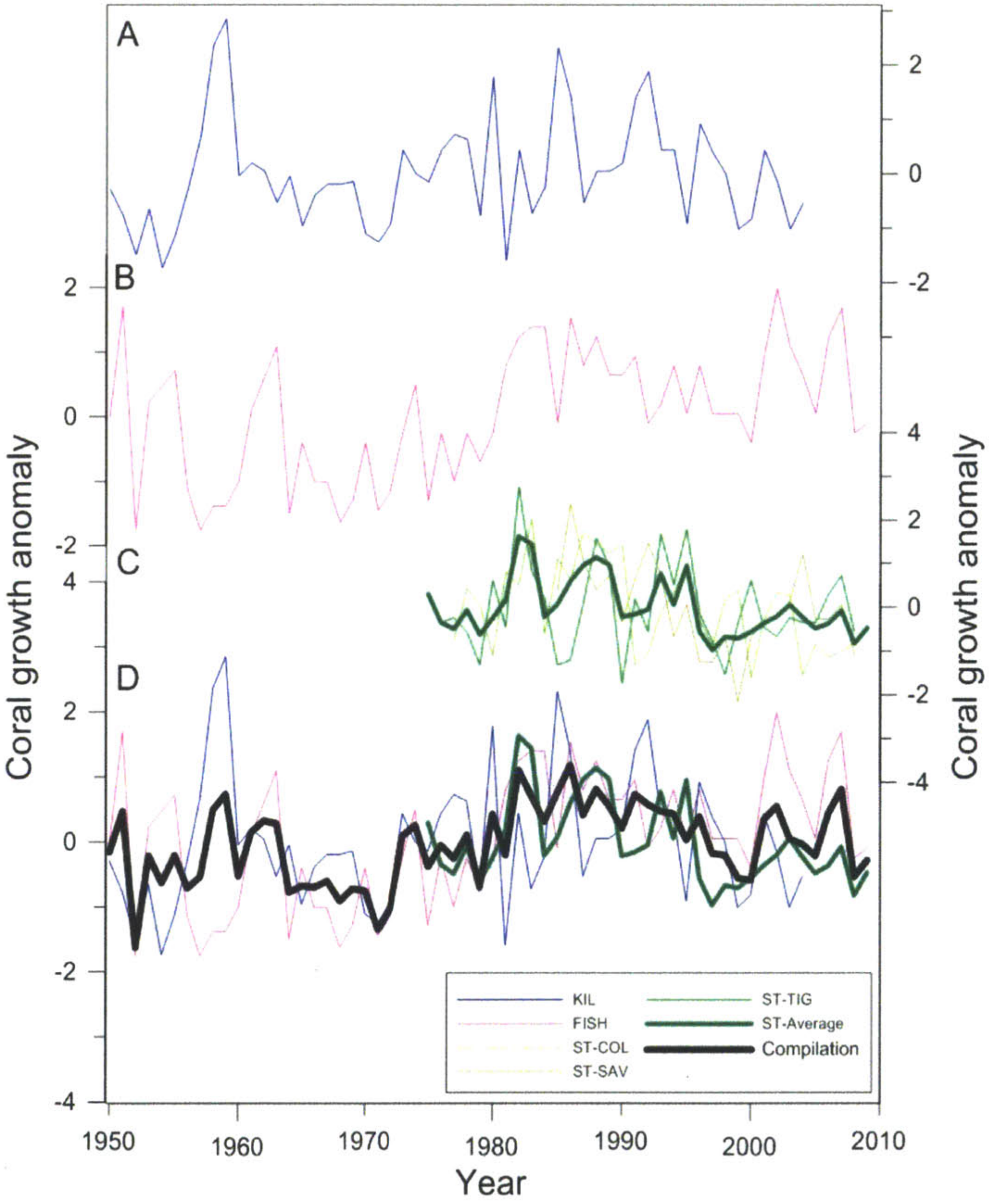

Figure 11. Coral records used to construct the Eastern Caribbean growth chronology. **A** Puerto Rico coral growth from *Kilbourne et al., 2010* (KIL), **B** USVI coral growth from Fish Bay (FISH), **C** Thin lines represent individual coral growth records from College Shoals (ST-COL), Savana (ST-SAV) and Tiger Bay (ST-TIG), the thick green line shows the average coral growth for these records collected from St. Thomas (ST-Average) **D** Thin colored lines represent the individual coral growth records listed in A-C, the thick black line represents the East Caribbean growth compilation.

(b) West Caribbean

Figure 12. Site locations for corals collected in Belize, the Yucatan and the Bahamas.

The West Caribbean chronology was calculated using 5 different corals collected from the Bahamas, the Yucatan and Belize (figure 12). The 3 cores from the Yucatan were first averaged to construct a chronology from the Yucatan (YUC). Annual growth rate anomalies were then averaged for the records from the Yucatan, Belize and Bahamas (figure 13). The 5 cores were sufficiently long to allow for an overlap of 40 years between cores. Although these corals come from very different geographical regions, spanning roughly 1000km, the correlations between cores are remarkably similar, especially in comparison to the correlations between cores located in much closer proximity in the Eastern Caribbean (Tables 3,4). Although the correlations are lower between records from the Yucatan peninsula and the Bahamas, the removal of the Bahamas record in the final chronology does not significantly affect the chronology (Comp 6; figure 14, table 5).

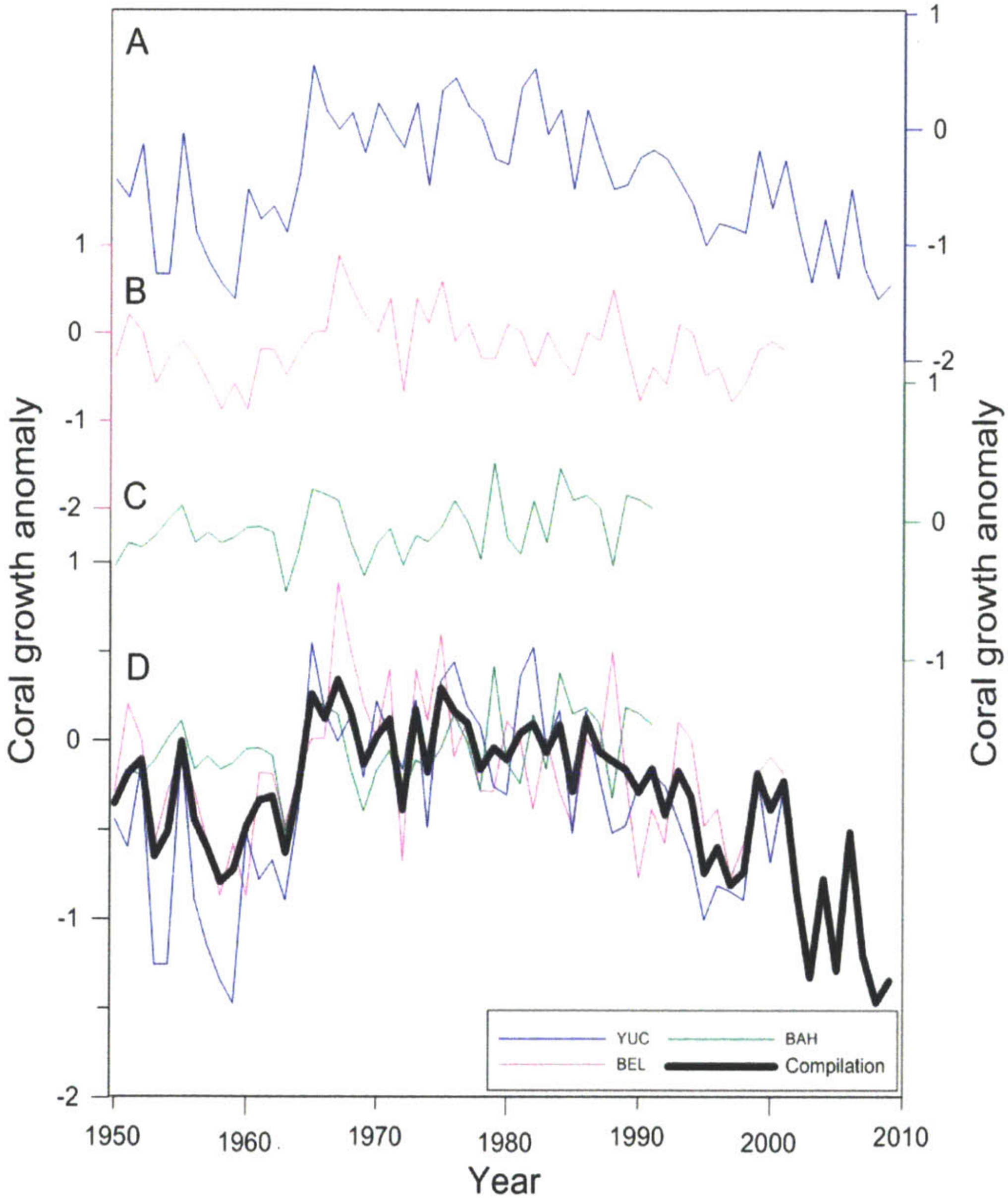

Figure 13. Coral records used to construct the Western Caribbean growth chronology. **A** Yucatan coral growth (YUC), **B** Belize coral growth (BEL), **C** Bahamas coral growth (BAH), **D** Thin colored lines represent the individual coral growth records listed in A-C, the thick black line represents the growth compilation.

Table 4. Correlation coefficients between coral time series from the Western Caribbean over the period of greatest overlap between individual records and between the coral time series and the West Caribbean master chronology index over the period 1950-1991.

Coral ID	YUC	BEL	BAH
YUC	-		
BEL	0.513	-	
BAH	0.3	0.0256	-
West Caribbean Index	**0.915**	**0.632**	**0.32**

Standard error for each growth chronology was calculated based on the standard deviation of the site averaged growth chronologies.

$$Standard\ error = \frac{standard\ deviation}{\sqrt{\#\ of\ records}}$$

It is important to note that the error associated with the individual records, which is based on the standard error between separate tracks used to calculate the final extension rates for the individual records, was not included in the error calculations associated with the master chronologies. As a result, the errors displayed are slightly smaller than the actual error associated with each chronology.

A seven-year moving average was used as a smoothing filtering technique to reduce the variance at high frequencies (Chatfield, 1996; Dodge and Lang, 1983; Fritts, 1976).

3.2.2. Importance of multiple records

Future studies examining the relationship between coral growth and environmental parameters should systematically collect sufficient cores for statistical analyses. For tree-ring analyses, the International Tree-Ring data bank requires that data be replicated in a minimum of 10 different trees and recommends that at least two cores are taken per tree (Fritts, 1976). Larger sample sizes not only decrease the standard error associated with the master chronology but mitigate the effects of human error such as missing annual growth bands, counting sub-annual stress bands, etc. Likewise, *averaged* growth chronologies consisting of multiple individual coral records provide the best record of large-scale environmental processes because the growth variation that is associated with these processes, which are common to all growth records, is emphasized when averages are made. Furthermore, the effects of non-climactic factors (such as species differences, age, reproduction, etc) which differ among individual corals and from site to site are minimized by the averaging process (Fritts, 1976).

The current study was limited by the number of available cores and the variability in the temporal scales of each of the individual cores. As such, the constructed index chronologies tend to be most highly correlated to a particular record; the Western Caribbean index is most highly correlated to the records from the Yucatan (r=0.915) and Belize (0.632), and the Eastern Caribbean index is most highly correlated to the record from Puerto Rico (r=0.685) and two of the records from the USVI (FISH: r= 0.572, COL: r=0.677).

Several master chronologies were constructed omitting certain records as a test of the influence on any particular record on the final chronology (figure 14). It is important to note that the amplitude of the coral growth anomaly does vary slightly depending on the records used to construct the master chronologies for the East and West Caribbean, and occasionally significantly depending on the inclusion or omission or certain single records. In the Eastern Caribbean, the omission of either FISH or KIL makes a significant difference to the record pre-1970. Both of these records were included for the final compilation.

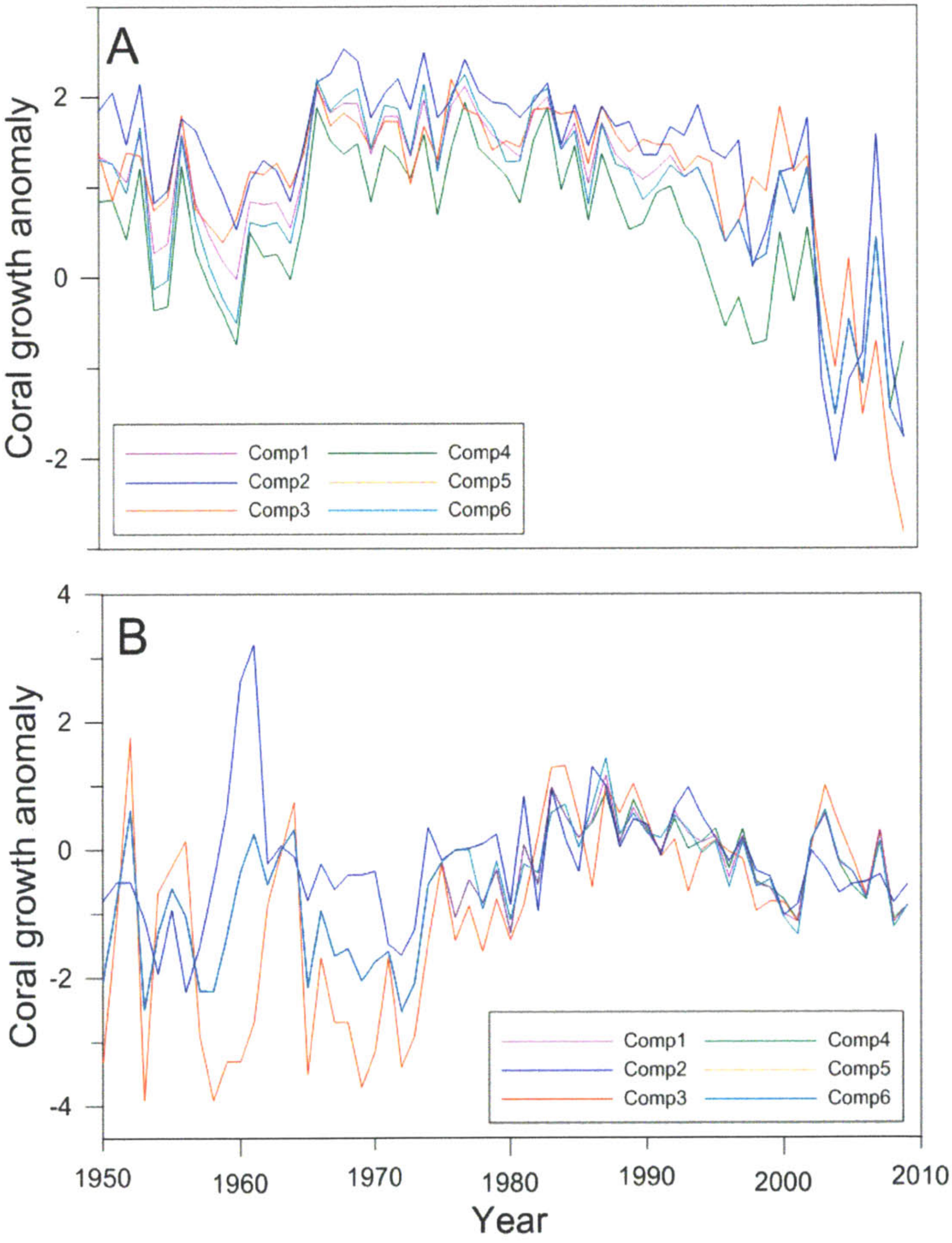

Figure 14. (A) Compilations constructed for the Western Caribbean (A) and the Eastern Caribbean (B) with the omission of certain individual records (see table 5(A), (B), respectively).

Table 5. Compilations constructed excluding individual records for (A) the Western Caribbean compilation and (B) the Eastern Caribbean compilation. Blank spaces represent the records which were omitted for each compilation.

(A)	**JAR A**	**MAR A**	**MAR B**	**BEL**	**BAH**
Comp1	**X**	**X**	**X**	**X**	**X**
Comp2	-	X	X	X	X
Comp3	X	-	X	X	X
Comp4	X	X	-	X	X
Comp5	X	X	X	-	X
Comp6	X	X	X	X	-

(B)	**FISH**	**KIL**	**COL**	**SAV**	**TIG**
Comp 1	**X**	**X**	**X**	**X**	**X**
Comp 2	-	X	X	X	X
Comp 3	X	-	X	X	X
Comp 4	X	X	-	X	X
Comp 5	X	X	X	-	X
Comp 6	X	X	X	X	-

3.3 Environmental Records

SST records for the period 1900-2009 were obtained from the 2°x2° gridded National Oceanic and Atmospheric Administration (NOAA) Extended Reconstructed Sea surface Temperature (ERSST) version 3b climatology which is based on observations from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) *(NOAA/OAR/ESRL PSD, Boulder, Colorado, USA).* Regional SST boxes were obtained by averaging SSTs over set geographical regions, eg. Caribbean box (16-25N, 86-59W). Chlorophyll-a data were obtained from the SeaWIFS website (http://oceancolor.gsfc.nasa.gov/SeaWiFS/).

3.4 Climate Models

To study the relationship between coral growth and wide-scale oceanographic parameters such as current direction, wind strength, temperature, salinity and sea level pressure, I made use of data available from the Simple Ocean Data Assimilation (SODA) Reanalysis (Carton and Giese, 1999). A reanalysis climate model is one which is highly constrained by data assimilation and historical observations. The observations that constrain the model can be both comprehensive for example, those variables measured by satellite, as well as relatively sparse, for example measurements of sea level pressure. The reanalysis model, essentially interpolates between observations in a physically consistent way resulting in a gridded and complete dataset. It is important to keep in mind, however, that the spatial consistency and quality of the data has change over time, with the most comprehensive data available after the advent of the satellite era (ie. post 1980). Pre-1980, the data is mostly from a network of in-situ measurements. Although reanalysis data are considered to be more accurate than pure model output data, they should nevertheless not be considered to be true observations.

The latest version of the SODA Reanalysis (v2.2.4) was just released and includes monthly gridded data from 1871-2008. The model has an average spatial resolution of 0.25° x 0.4° with 40 depth levels. The output is produced by an ocean general circulation model (OGCM) which is constrained by observations with corrections occurring approximately every 10 days. The surface forcing includes winds from the NCEP/NCAR reanalysis which are bias corrected by comparison with COADS winds and the evaporation/precipitation is obtained from the Xie-Arkin climatology. Assimilated observations include almost all available hydrographic profile data, as well as ocean station data, moored temperature and salinity time series, surface temperature and salinity observations of various types, and nighttime infrared satellite SST data. The output is in monthly-averaged form, mapped onto a uniform 0.5 x 0.5°, 40-level grid (Carton & Giese, 2008; Carton et al., 2000).

3.5 Matlab Composite Analyses

To get an idea of how conditions in the Caribbean vary with large-scale modes of climate variability, including the PDO, a composite function was used to average the spatially variable climactic parameters for two different conditions (1) years when PDO was in its 'positive' phase and (2) years when PDO was in its 'negative' phase. A threshold was set to recognize a 'positive' PDO event as one in which the PDO anomaly was greater than 0.5, and a 'negative' PDO event as one in which the PDO anomaly was less than -0.5. The function goes through the PDO index and highlights the years where the above conditions are met and then averages the oceanic parameters during those years. To highlight the difference in the oceanographic conditions between these two phases, a composite difference was calculated. These analyses were repeated using the coral growth rate time series to visualize the oceanographic parameters when corals were growing most.

4. Results & Discussion

Part I. A Study of Caribbean Climatology using SODA Reanalysis

Seasonal Trends in the Caribbean Basin

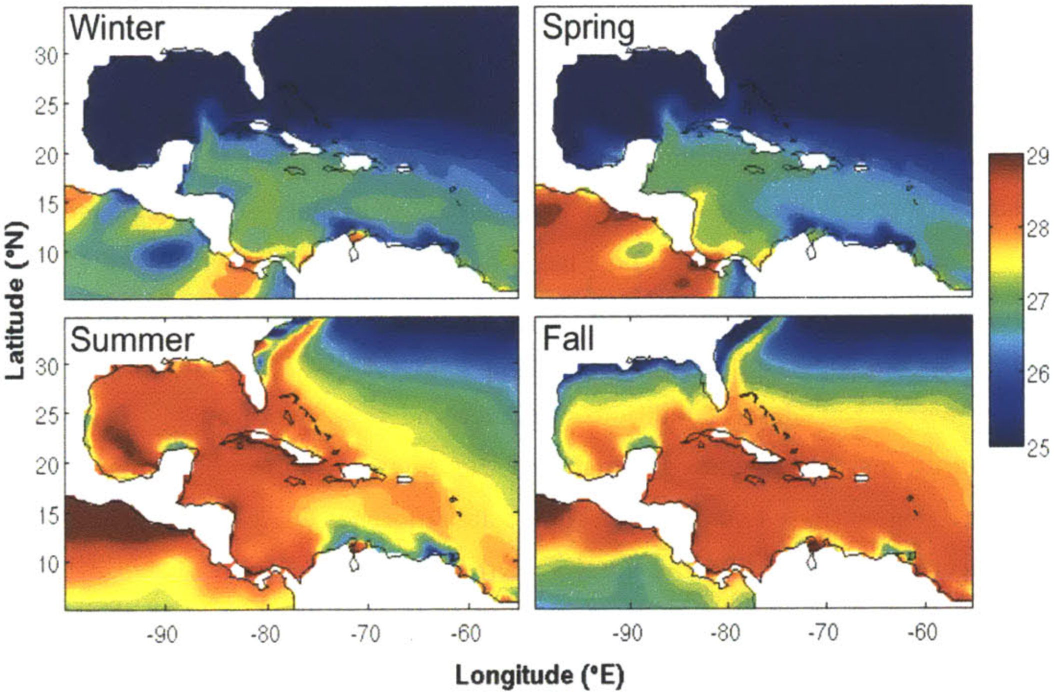

Figure 15. Average sea surface temperature in degrees Celsius for each season 1900-2008. Winter (December, January, February), Spring (March, April, May), Summer (June, July, August), Fall (September, October, November).

Annual temperatures in the Caribbean basin range from 25 to 29°C (figure 15). Much of the Northern half of the basin (north of the Antilles) and the Gulf of Mexico experience the full 4 degree range of these temperatures whereas the Southern basin experiences a smaller range of temperatures on the order of 1-2°C. The Western Caribbean region, close to the Yucatan peninsula, has average winter temperatures of approximately 26.5-27°C and average summer temperatures between 28-29°C. The Eastern Caribbean islands of Puerto Rico and the USVI lie on the boundary of the extreme winter temperatures, with the northern sides of the islands (low of <26°C) experiencing a 0.5 degree difference in winter temperatures than the southern sides of the islands (low of ~26.5°C). Colder, upwelled water is visible off the northern coast of South America in the Winter, Fall and Summer and on the Northern section of the Yucatan Peninsula in the Summer.

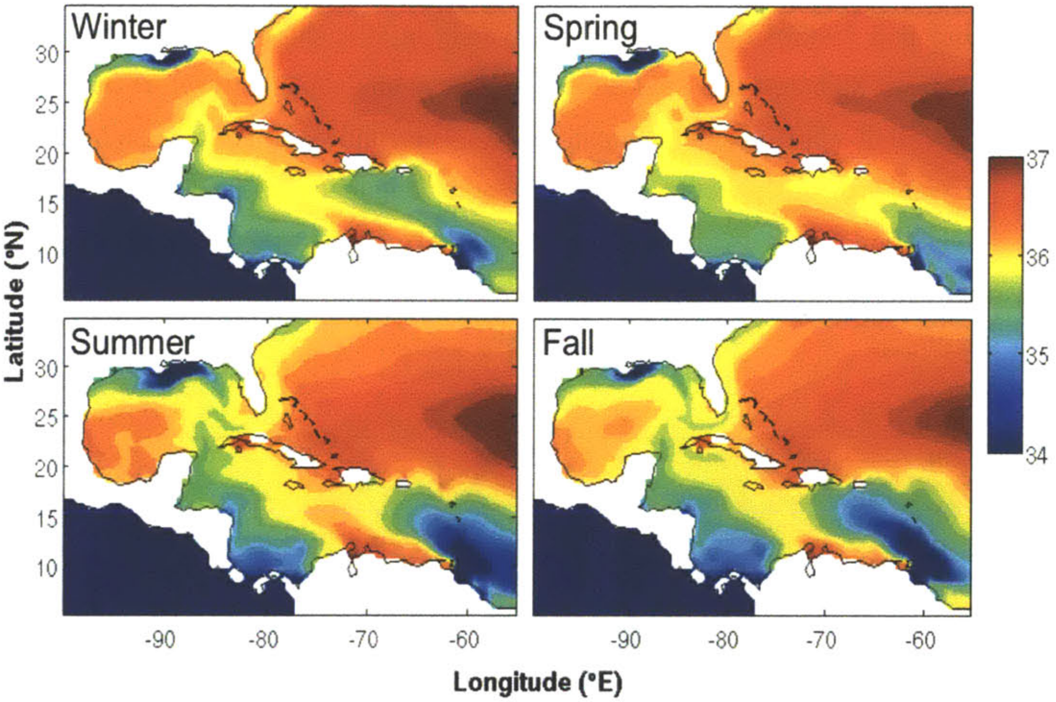

Figure 16. Average sea surface salinity in psu for each season 1900-2008.

Sea surface salinity in the Caribbean basin is mostly constant through out the year and ranges from 36 to 37 psu (figure 16). This is most likely because the Caribbean basin lacks a predominance of evaporation over precipitation (Gordon, 1967). Regions experiencing the greatest salinity variations are located near the outflow of major rivers such as the Mississippi in the Gulf of Mexico, and the Orinoco and Amazon rivers in South America. The Mississippi outflow is relatively constant with the greatest freshwater input to the Gulf occurring during the summer months. The outflow from the Orinoco is greatest in the Summer and fall months with the associated salinity minimum penetrating as far north as Southern Puerto Rico in the Fall months of September, October and November. There is also a freshwater flux, presumably associated with the Panama Canal in the Columbian Basin which is freshest in the Summer and Fall. The western Caribbean region, near the Yucatan Peninsula, has highest salinities in the Spring (36psu) and lowest salinities in the Summer and Fall (~35psu). Similar to the trends in SST, the eastern Caribbean islands of Puerto Rico and the USVI, lay on a salinity boundary between relatively lower salinities of approximately 36psu and higher salinities between 36.5 and 37psu. As was previously noted, the freshwater tongue from the Orinoco and Amazon rivers penetrates as far north as the southern sides of these islands in the Fall brining waters with salinities of approximately 35psu and lingering in to the Winter months.

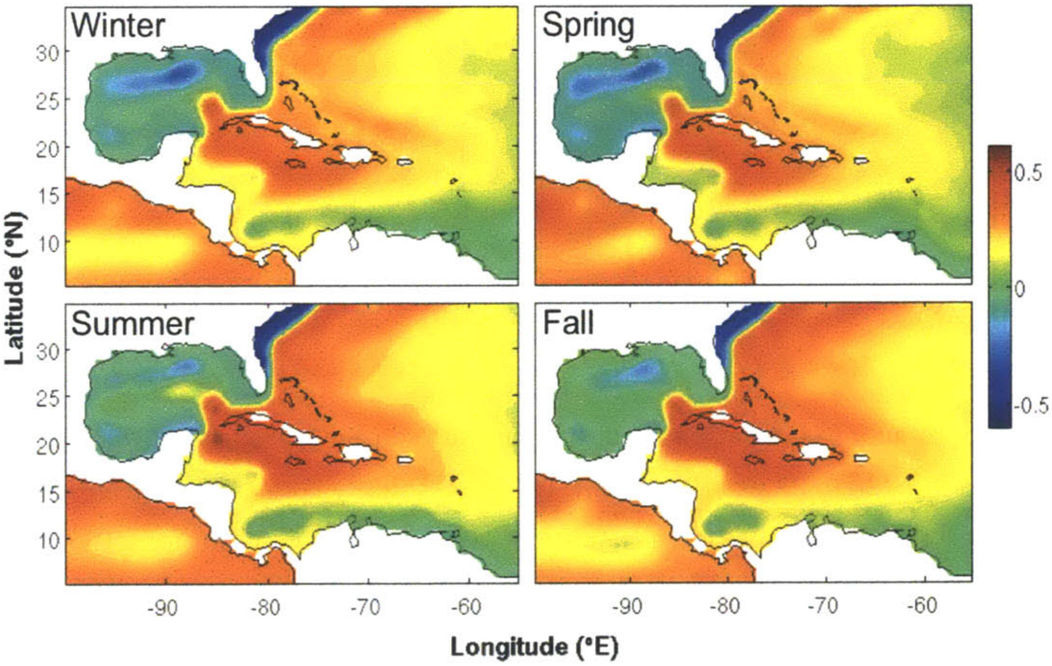

Figure 17. Average sea surface height in meters for each season 1900-2008.

Sea surface height (SSH) in the Caribbean does not vary much during the year (figure 17). The predominant pattern of high SSH in the region south of Cuba and Hispañola is visible in all seasons with maximum SSHs occurring in the summer, most likely due to high temperatures and trade wind strength during these months. SSH is lowest in the Gulf of Mexico and along the US eastern seaboard.

SSH plays an important role in ocean circulation and in the absence of wind (ie. pure geostrophic flow), the boundaries between SSH anomalies would represent the mean surface flow (at 90° to the right of the potential difference). There are two main factors that control potential difference in the ocean, (1) wind and (2) thermohaline variations. In the Caribbean Basin, the winds play an integral role in surface circulation because the area lacks temperature extremes and a predominance of evaporation over precipitation, which would result in thermohaline convection (Gordon, 1967). Instead, circulation is driven by a combination of geostrophic flow and wind stress. There are three possible interactions between wind stress and geostrophic flow, (1) no wind => there is pure geostrophic flow, (2) the direction of wind stress is opposite to the geostrophic gradient => the flow is "down slope", (3) the direction of wind is in the same direction as the geostrophic gradient => the flow is "uphill". In the Caribbean, the latter condition applies as the Trade Winds cross the basin in the direction of geostrophic flow which results in the Caribbean current gaining energy and dynamic height as it moves westward (Gordon, 1967).

The Caribbean wind field is dominated by the Easterly Trade Winds which are strongest between 10-25°N. The Trades are strongest in the Caribbean during the Summer months (figure 18) with the greatest magnitude winds occurring south of Cuba and Hispañola. In the Winter, the trades are slightly more Northeasterly than the rest of the year. Likewise, in the region near the Yucatan Peninsula, wind direction changes between the summer and spring months when the dominant wind direction is northward and the winter and fall months when the dominant wind direction is southward. The region between 30-35°N sees the largest seasonal changes in wind direction and strength, with the strongest N-Easterly winds occurring in the Fall and a complete reversal of wind direction in the winter and spring. As was mentioned previously, winds are the dominant control on Caribbean surface circulation and affect the flow to a depth of 1000-1500meters (Gordon, 1966).

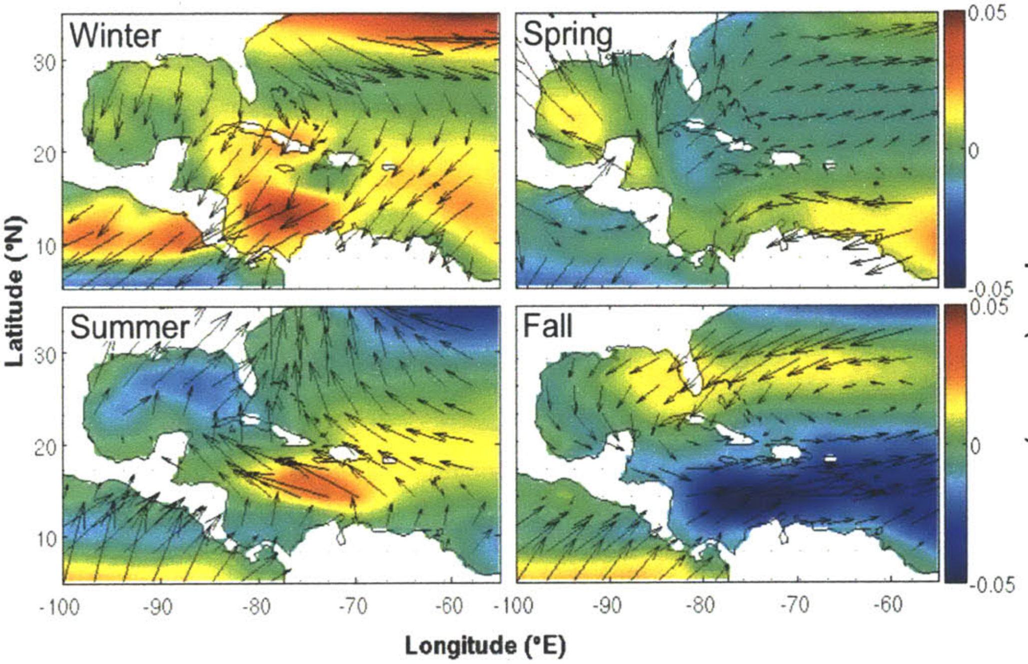

Figure 18. Seasonal wind field anomalies calculated by subtracting the annually averaged climatology from the seasonally averaged climatology for the period 1900-2008. Black arrows depict wind direction, colors represent the magnitude of the wind.

Caribbean currents are mainly eddy driven meaning that seasonal anomaly maps appear to be slightly chaotic (figure 19). What is most striking is the seasonal change in the strength of the Caribbean current, which is strongest in the Summer months and weakest in the Spring. Currents off of South America appear to be strongest in the Spring and Summer months corresponding to the increase in Trade wind strength during this time.

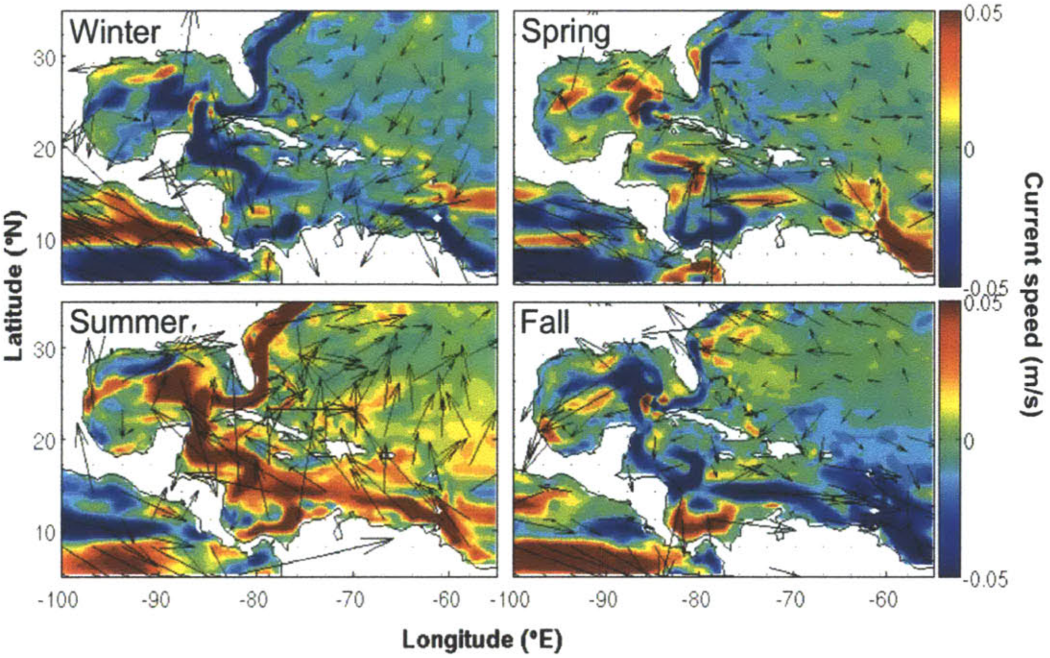

Figure 19. Seasonal wind field anomalies calculated by subtracting the annually averaged climatology from the seasonally averaged climatology for the period 1900-2008. Black arrows depict wind direction, colors represent the magnitude of the wind.

Chlorophyll concentration provides an estimate of the live phytoplankton biomass in the surface layer and hence, an indication of the availability of nutrients. The Caribbean basin is predominantly oligotrophic but is highly influenced by riverine inputs from some of the worlds major rivers including the Amazon and Orinoco and coastal upwelling along the southern margin of the basin (Bonilla et al., 1993). The influence of the Amazon and Orinoco rivers on chlorophyll concentration is highest in the spring and summer months (figure 20). The effects of coastal upwelling are visible along the southern margin year round, but are strongest from January-May. The frequency of upwelling blooms decrease after July but at this time the Orinoco river plume expands over much of the Eastern Caribbean basin reaching Puerto Rico around September-October (Müller-Karger et al., 1989). Chlorophyll blooms are also visible along the western margin, particularly around Honduras/Nicaragua and the northern section of the Yucatan Peninsula.

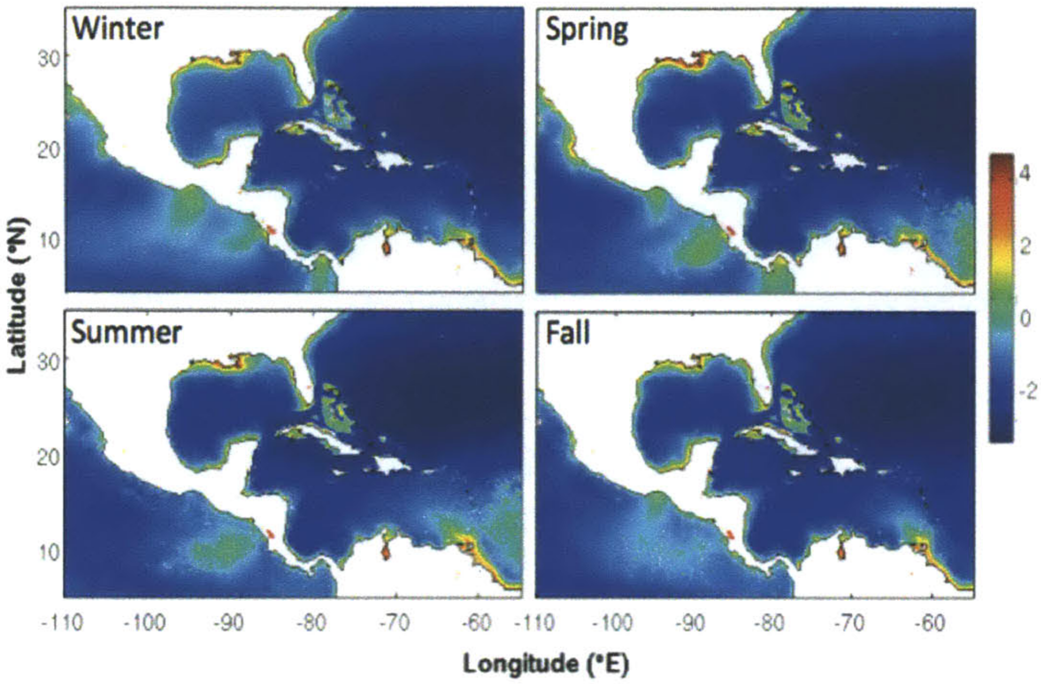

Figure 20. Average Chlorophyll concentration for each season 1900-2008.

The large-scale chlorophyll distribution in the Caribbean is controlled largely by wind stress, the flux of water into the basin and river discharge. During the first half of the year, advection of water from the Atlantic dominates which restricts phytoplankton blooms to the southern half of the Caribbean, and flushes the northern and central areas. During the second half of the year, this influx is decreased and Trade-Wind driven Ekman transport dominates encouraging the north-westward propagation of surface waters through out the basin.

Influence of the AMO and PDO on the Caribbean

Caribbean SST is most strongly linked to the AMO, which is unsurprising as the AMO is predominantly a mode of Atlantic SST variability (figure 21). SSTs throughout the Caribbean basin are strongly positively correlated to changes in the AMO with periods of positive (negative) AMO corresponding to periods of higher (lower) SST. The PDO is only weakly correlated to SSTs in the Caribbean Basin; over most of the

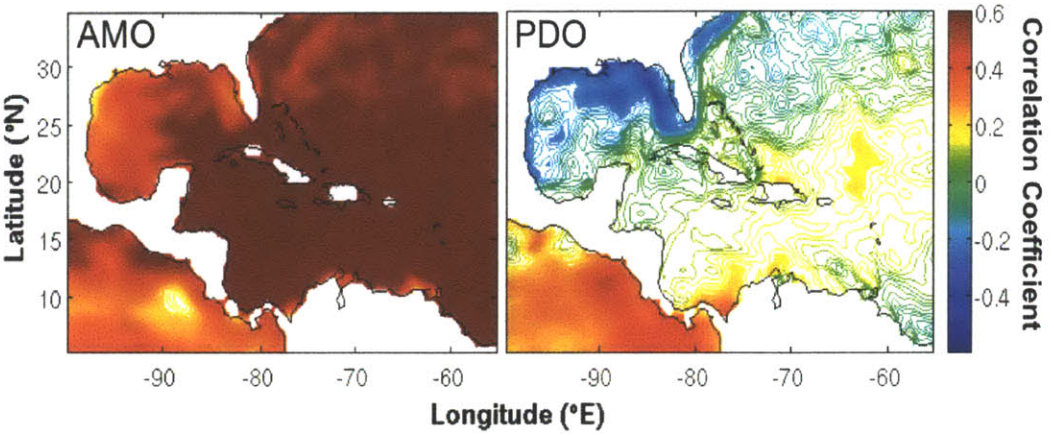

Figure 21. Correlation coefficients between AMO and PDO and sea surface temperature in the Caribbean basin 1900-1980. Solid colors depict correlation coefficients at the 95% confidence interval, colored contours depict correlations below this confidence interval.

central region of the basin there is a weak positive correlation between PSO and SST, but in the Gulf of Mexico and off the Northern coast of South America, the correlation is weak and negative. This could be due to the influence of precipitation and river runoff in these areas and upwelling off the coast of South America during periods of positive PDO. Atlantic SST's are associated with the PDO through atmospheric teleconnections involving changes in the surface latent heat flux due to variations in the trade wind strength which are influenced by ENSO (and PDO on long time scales) (Klein et al., 1999).

The AMO is strongly positively correlated with salinity over some of the eastern Caribbean and the western tropical Atlantic which is unsurprising as higher SSTs promote evaporation, which in turn, increases sea surface salinity (figure 22). PDO is negatively correlated with salinity in the region north of Cuba, which encompasses the Bahamas. This may be due to the influence of wind stress in this area which is also inversely correlated to SST; stronger winds promote evaporation which increases salinity. The PDO is also positively correlated to salinity in the Orinoco runoff region, this could either be due to the influence of heightened winds or through diminished precipitation or runoff.

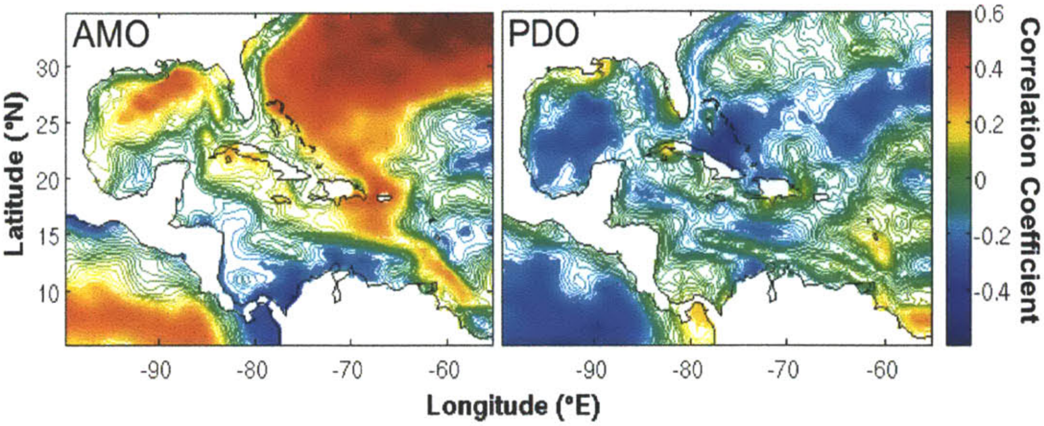

Figure 22. Correlation coefficients between AMO and PDO and sea surface salinity in the Caribbean basin 1900-1980. Solid colors depict correlation coefficients at the 95% confidence interval, colored contours depict correlations below this confidence interval.

Sea surface height is largely related to changes in circulation (Talley et al., 2011). The AMO is strongly negatively correlated to SSH in the western part of the Caribbean basin, the gulf of Mexico and the Gulf Stream and very weakly positively correlated to SSH in the eastern basin. The AMO, is however, strongly positively correlated to SSH in the region north of the Orinoco runoff. PDO is positively correlated to SSH over much of the Caribbean basin, but in particular in the region of maximum SSH in the Caribbean (south of Cuba and Hispañola).

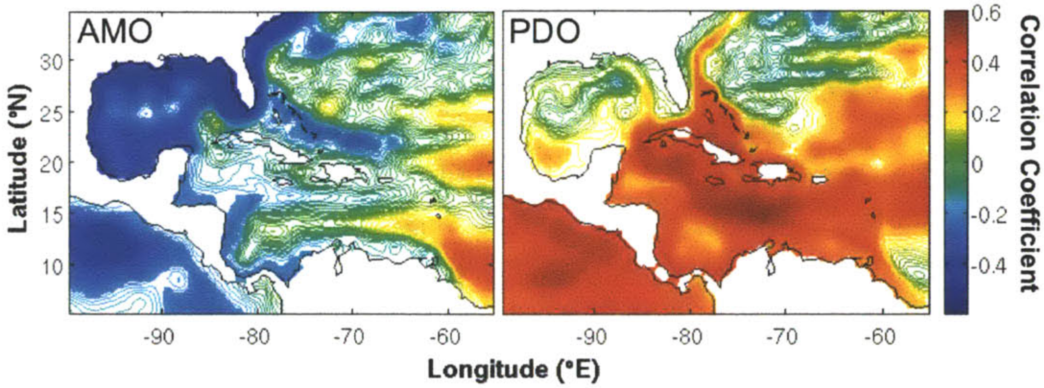

Figure 23. Correlation coefficients between AMO and PDO and sea surface height in the Caribbean basin 1900-1980. Solid colors depict correlation coefficients at the 95% confidence interval, colored contours depict correlations below this confidence interval.

Wind stress in the southern part of the Caribbean basin, reaching as far as the Yucatan Peninsula is inversely correlated to the AMO. This means that during periods of positive AMO, wind stress is weaker in this area. PDO is inversely correlated to wind stress in a latitudinal band extending across the central Caribbean. The PDO also influences wind stress off the northern coast of South America with periods of positive PDO corresponding to increased wind stress in this area.

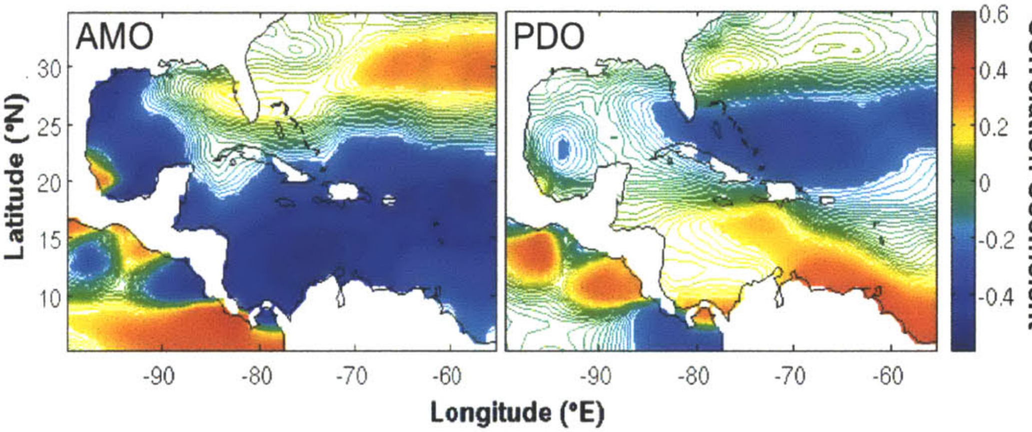

Figure 24. Correlation coefficients between AMO and PDO and wind speed in the Caribbean basin 1900-1980. Solid colors depict correlation coefficients at the 95% confidence interval, colored contours depict correlations below this confidence interval.

Decadal Trends in the Caribbean Basin

Linear regression trends for salinity, wind stress and sea surface height for the period 1900-2008 show different overall trends than for the period 1950-2008 (figures 25 and 26). The one exception to this is SST which increased over much of the basin during both time periods with certain areas such as the gulf of Venezuela and the eastern coast of the US showing the most dramatic heating. From 1900-2008 salinity in the Caribbean basin decreased along the western coast and portions of the north Caribbean, whereas salinity mainly increased in the central Caribbean and in certain spots such as near the out flow of the Orinoco and the Gulf of Venezuela (figure 25). From 1950-2008, salinity in most of the Caribbean basin

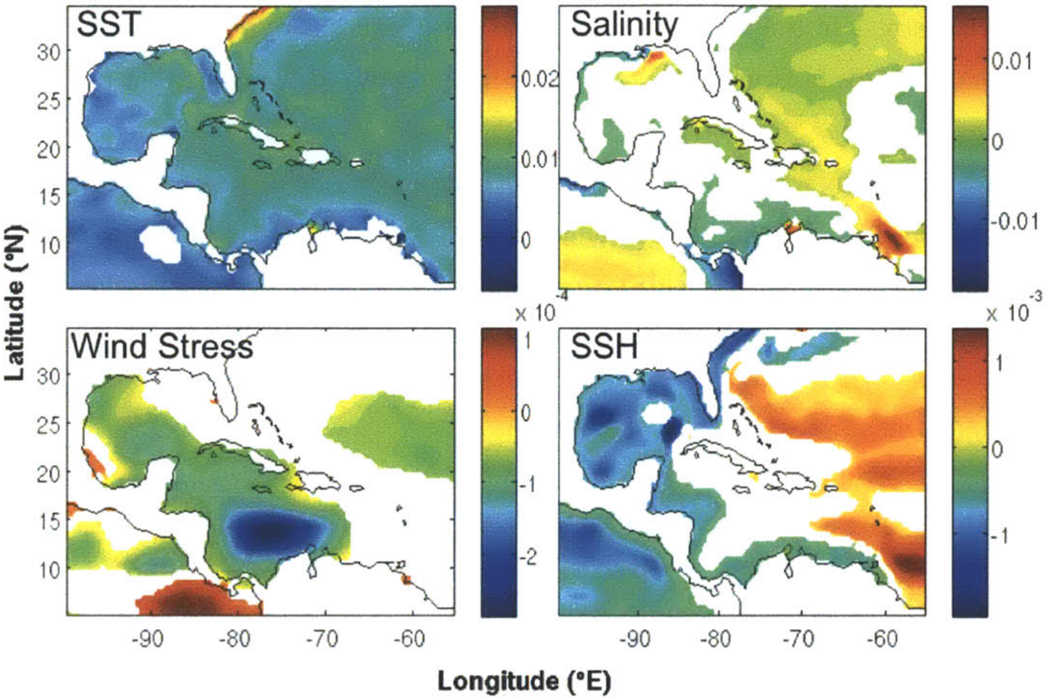

Figure 25. Linear regression plots depicting significant trends (at the 95% confidence interval) in sea surface temperature (SST), salinity, wind stress and sea surface height (SSH) over the period 1900-2008.

decreased indicating either an increase in precipitation over this period or a decrease in evaporation, but as SSTs are uniformly rising which should lead to increasing evaporation, the decrease in salinity over this period is most likely due to an increase in precipitation (figure 26). SSH decreased in the western part of the basin during the 1900-2008 period, but increased in the eastern part of the basin. In the 1950-2008 period, SSH predominantly increased, most notably in the area of maximum SSH south of Cuba and Hispañola. The recent increasing trend in SST may be a result of circulation changes associated with the AMO. The AMO is thought to be influenced by changes in the meridional overturning circulation (MOC), which transports heat from the tropics to the poles. Variations in MOC during this time, which are thought to affect circulation in the Caribbean (Jochum and Malanotte-

Rizzoli, 2001), may have resulted in the observed increase in SSH. Alternatively, the increasing SSTs may have contributed to thermal expansion of the surface layer.

The most striking difference in the trends in wind stress between the two periods are in the area of the Caribbean Low Level Jet (CLLJ). From 1900-2008, there is an overall weakening trend in the CLLJ, whereas from 1950-2008, wind stress is predominantly increasing. The period post 1950- marks the shift of the AMO from predominantly negative to predominantly positive. This may account for the strengthening of the CLLJ, as periods of positive AMO are associated with strengthening the CLLJ. Likewise, during this period the PDO also shifted from predominantly negative to positive. El Nino events, which are more prevalent during positive periods of the PDO, are known to strengthen the CLLJ during the summer (Taylor et al., 2002).

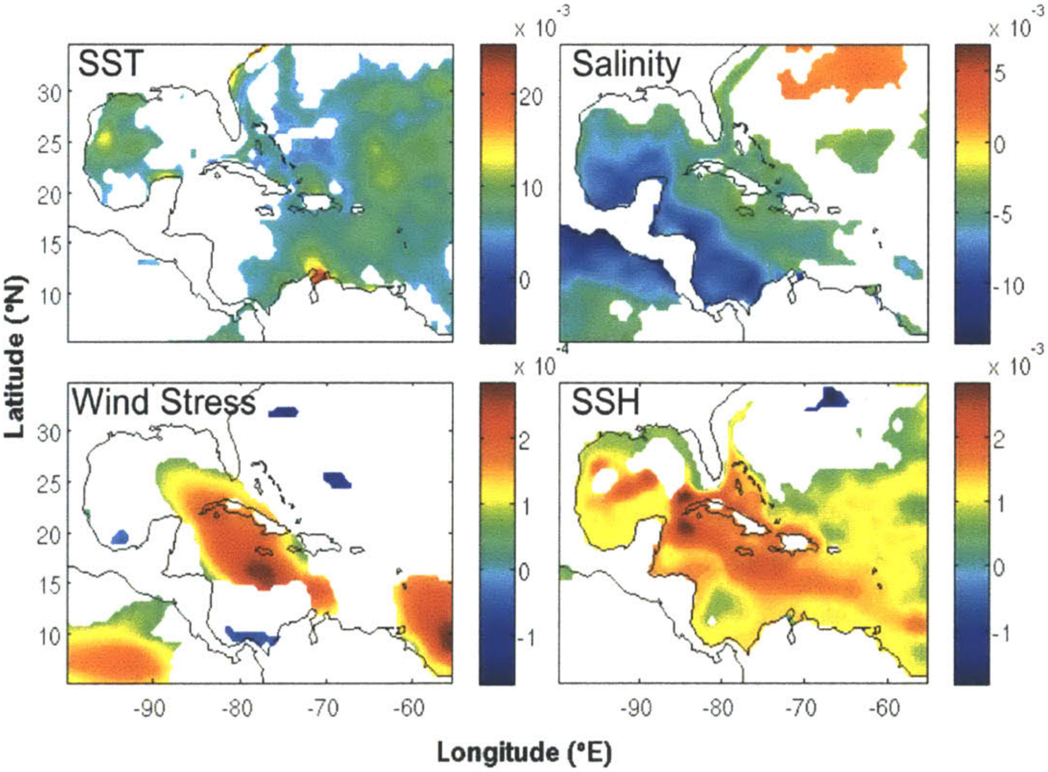

Figure 26. Linear regression plots depicting trends (at the 95% confidence interval) in sea surface temperature (SST), salinity, wind stress and sea surface height (SSH) over the period 1950-2008.

Part II. Climate Controls on Coral Growth in the Caribbean

Caribbean Coral Growth

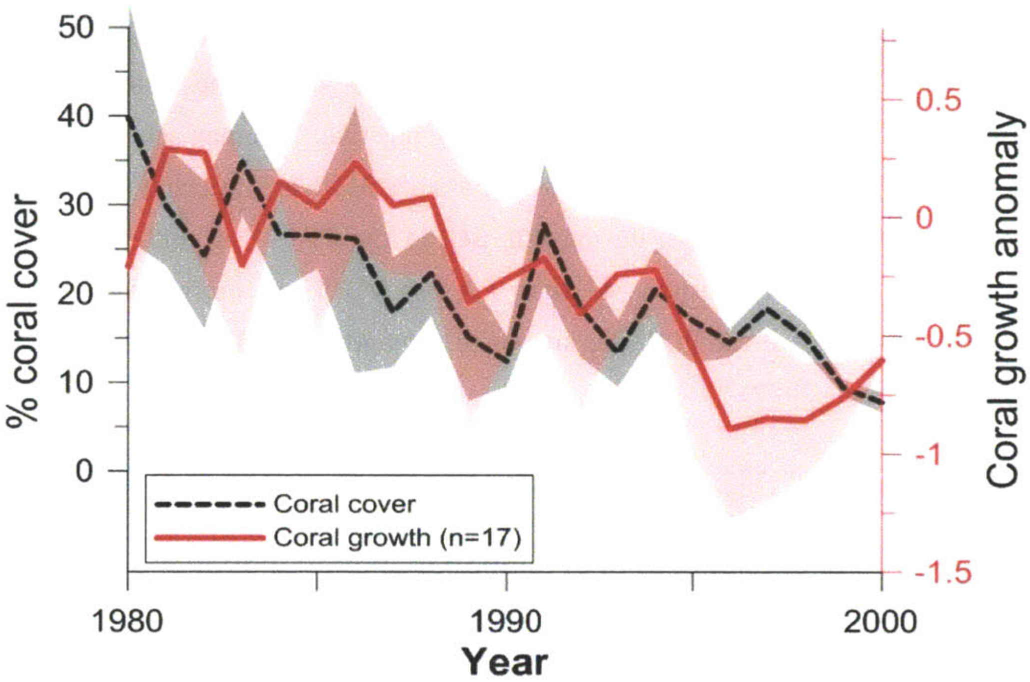

Figure 27. Caribbean coral growth over the same time period as the region wide decline in % coral cover. The dotted black line indicates % coral cover, the pink line is the Caribbean coral growth compilation using a total of 17 growth records. Shaded areas denote standard error.

Caribbean coral cover and architectural complexity collectively declined during the 20 year period between 1980 and 2000 (Gardner et al. 2003; Hughes 1994; Alvarez-Filip et al. 2011; Buddemeier et al. 2011). Likewise, averaged Caribbean coral growth for the entire Caribbean and Bermuda also declined over this period and shows a strong correlation with the decline in % coral cover ($r=0.58$, $p<0.01$) (figure 27).

A different picture emerges, however, when growth rate compilations are examined over a longer period of time, from 1950-2010 and are constructed separately from different environmental regimes in the Caribbean (figure 28). We constructed two growth rate records using corals we collected in the field, one for the Eastern Caribbean region (USVI & Puerto Rico) and one for the Western Caribbean (Yucatan, Belize, Bahamas) based on the geographical locations of the coral specimens as well as their relationship to temperature.

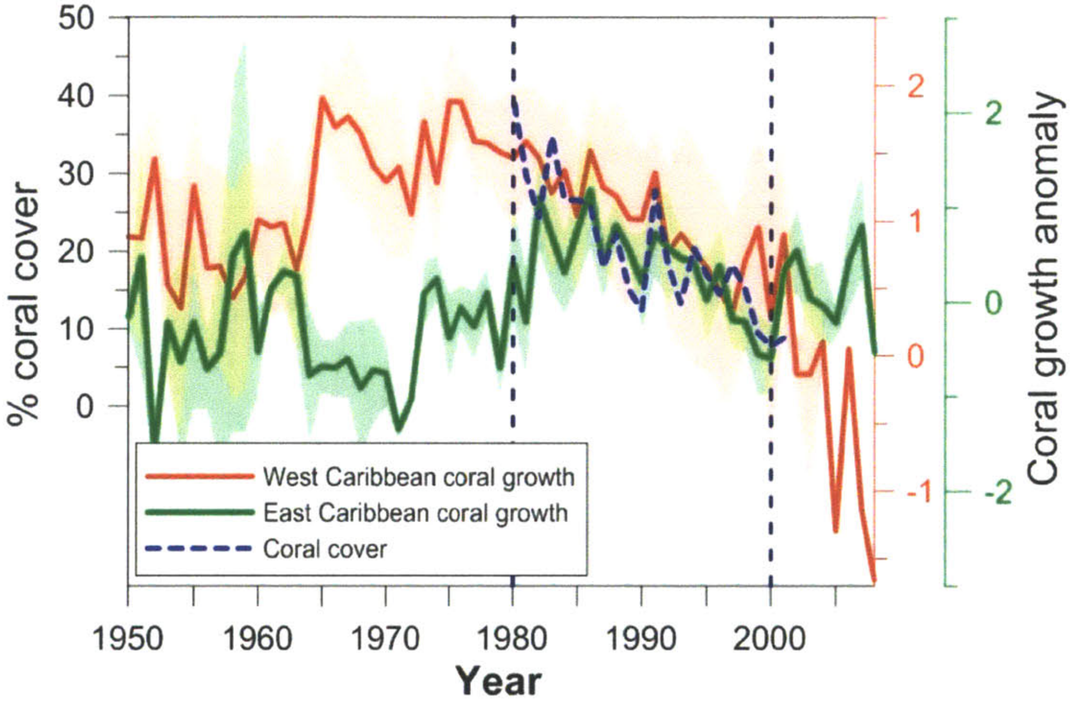

Figure 28. Percent coral cover (dashed blue line) plotted against East (green line) and West (blue line) Caribbean growth records for the period 1950-2010. Vertical blue dashed lines bracket the period of the region-wide decline in coral growth outlined in Gardner et al. (2003). Shaded lines denote the standard error associated with the coral growth records.

From 1950-1965 coral growth rates in both the Western and Eastern Caribbean were relatively stable, with Eastern Caribbean growth rates showing a slight increase. In ~1965 the records diverge, with East Caribbean growth rates showing a sharp decline and West Caribbean growth rates increasing suddenly. In the period leading up to 1980, East Caribbean coral growth rates increase steadily, whereas Western Caribbean growth rates begin to decline. This decreasing trend, for the Western Caribbean continues through the 1980-2000 period up until 2010.

Growth rates in the Eastern Caribbean begin to decrease around 1982, but then level off in the period between 2000-2010. These different responses raise important questions as to the underlying factors responsible for influencing coral growth. We examine the impacts of large-scale modes of climate variability and temperature on coral growth rates in both areas which sets the scene for whether or not corals are able to withstand extreme episodic events.

Coral Growth Rates and Temperature

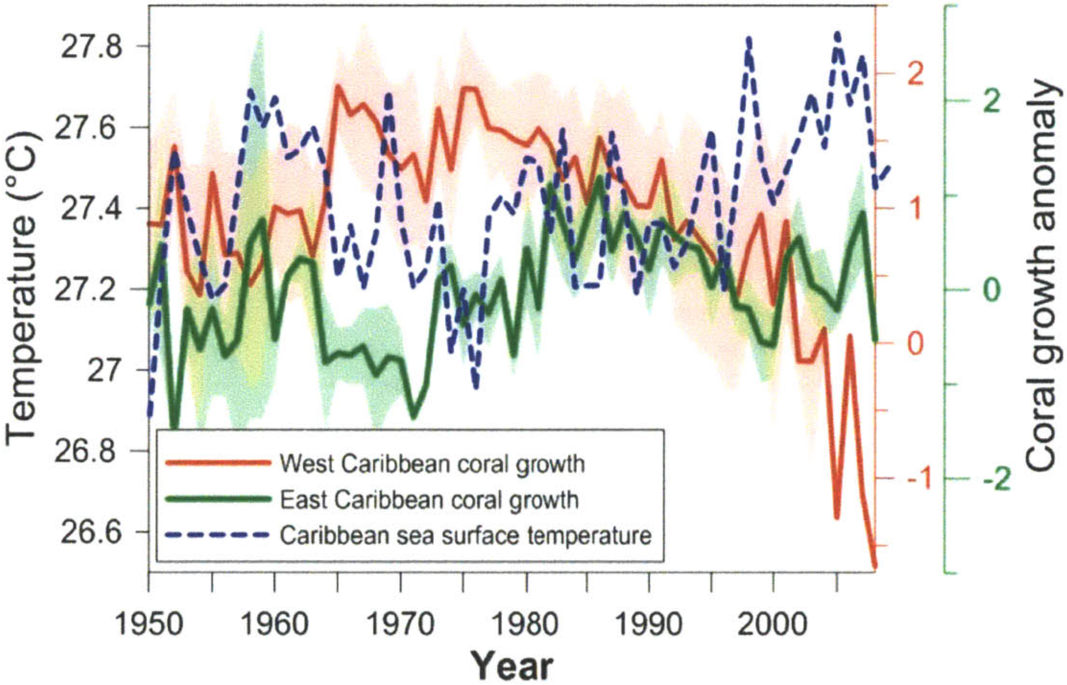

Figure 29. Caribbean sea surface temperature, calculated as the average SST in the region 16-25N, 86-59W (dashed blue line) plotted against East (green line) and West (blue line) Caribbean growth records for the period 1950-2010. Shaded lines denote the standard error associated with the coral growth records.

Several studies suggest that there is a fundamental dependency of coral growth rate on temperature (Marshall & Clode, 2004; Coles and Jokiel, 1978, Jokiel and Coles, 1977; Clausen and Roth, 1975). Indeed, several studies of long-term Caribbean coral growth have indicated a significant relationship between coral growth and temperature, including some of the studies from which records have been assimilated for the present analyses (Saenger et al. 2009, Carricart-Ganivet, 2004, Vasquez-Bedoya et al., 2012). However, we find that while coral growth rates from individual sites may exhibit a strong correlation with temperature variations (e.g. Vasquez-Bedoya et al., 2012), growth rates across our Caribbean sites do not exhibit a consistent relationship to temperature variability (figure 29).

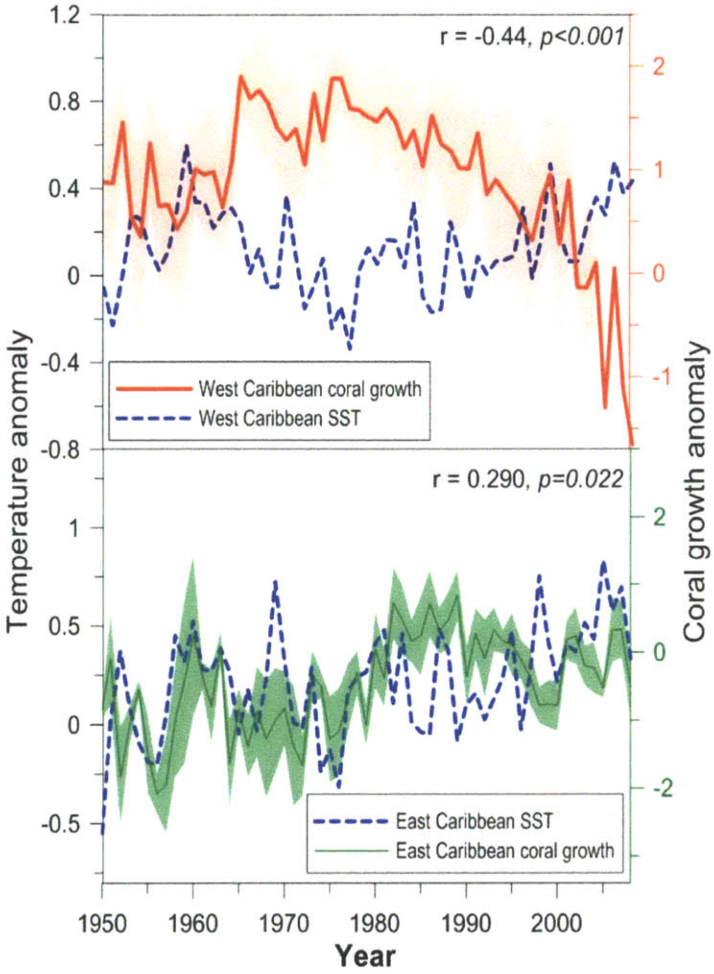

Figure 30. Records of East and West SST calculated as the average SST in the regions 18-20N, 64-68W and 12-22N, 86-76W, respectively (dotted blue lines) plotted against East (green line) and West (blue line) Caribbean growth records for the period 1950-2010. Shaded lines denote the standard error associated with the coral growth records.

Coral growth records from the Western Caribbean show a significant (r=-0.44, p<0.001) *inverse* relationship with sea surface temperatures from the Caribbean region (figure 29) and the Western Caribbean (figure 30). In contrast, coral growth rates from the Eastern Caribbean show only a weakly significant (r=0.383, p=0.002) but *positive* relationship with sea surface temperatures from the Caribbean region (figure 29) and the Eastern Caribbean region (figure 30). The opposite relationship seen between coral growth rates and temperature in the East and West Caribbean could be due to several different mechanisms: (1) temperatures in the western basin could have exceeded the optimal temperature threshold, resulting in decreasing growth rates whereas temperatures in the eastern basin have not exceeded this threshold (figure 31); (2) while temperatures in the two areas are similar, the temperature optima for coral growth in the two regions could be different resulting in positive growth in the east and decreasing growth in the west (figure 32) (3) temperature is not the dominant control on coral growth rate in both areas.

The first mechanism is suggested by various laboratory studies, which have demonstrated that coral growth generally peaks within a narrow range of optimal temperatures (Clausen and Roth, 1975; Marshall and Clode, 2004; Coles and Jokiel, 1978; Jokiel and Coles, 1977). Although average annual temperatures in the Western Caribbean (27.9°C) are slightly higher than those in the Eastern Caribbean (26.5°C), it is unlikely that the temperature disparity is large enough to cause the decline seen in coral growth in the Western Caribbean. We see no evidence that corals in the Western Caribbean experienced accelerated declines in growth with the exception of the most recent part of the record, which is driven by a single coral from the Yucatan. Taking into account, however, that the growth-temperature relationship is inverse for the

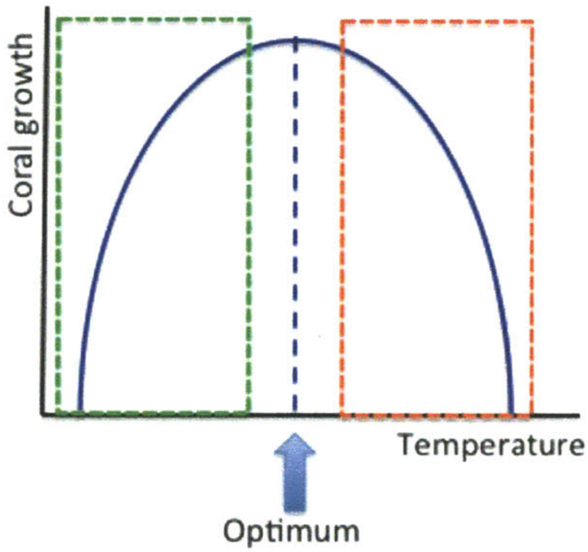

Figure 31. Schematic demonstrating the coral growth/temperature relationship. The optimum temperature for coral growth is depicted by the dotted blue line. The green (red) dotted box shows the possible relationship between coral growth and temperature in the East (West) Caribbean region.

entirety of our corals records, the longest of which extends more than 200 years (Vasquez-Bedoya et al., 2012), it is unlikely that the temperature threshold was crossed at some point before this and corals have maintained the inverse relationship with temperature ever since. Instead, most long-term growth studies indicate that corals are able to adapt to their ambient temperature regimes over extended periods of time, often up to 30°C (Coles et al., 1976; Coles & Jokiel, 1978). It is therefore, extremely likely that corals in the western Caribbean are adapted to their ambient, local temperature conditions.

The second mechanism takes into account this ability of coral species in different areas to be adapted to different temperature regimes, and as a result to have different temperature optima (figure 32). This is seen in Coles et al., (1976) where *Pocillopora damicornis* corals growing on Enewetok Atoll can withstand substantially higher absolute temperatures than their Hawaiian counterparts with a critical threshold of 35°C compared

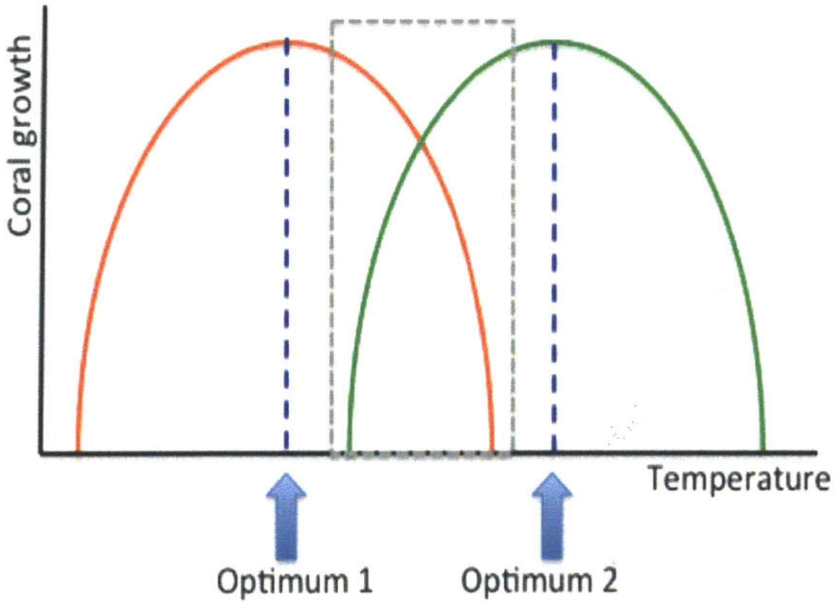

Figure 32. Schematic demonstrating the coral growth / temperature relationship for corals with two separate temperature optima. The green (red) curve shows the possible relationship between coral growth and temperature in the East (West) Caribbean region. The gray box indicates a possible scenario resulting in opposite growth

to 32.4°C for the Hawaiian species. They interpret this to mean that the natural temperature environment in which a coral lives is much more important to a coral's thermal tolerance than taxonomic distinctions. Indeed, *Siderastrea siderea*, the species common to both East and West growth chronologies - has been shown to be able to adapt, both physically and morphologically, to new environments (Foster, 1980) and to have a remarkable tolerance to extreme conditions (Muthiga & Szmant, 1987). In spite of this, however, studies suggest that that adaptation towards a distinct temperature optima and critical threshold requires a variation in ambient SST of at least a couple of degrees Celsius. This is clearly not the case, as mean annual temperatures across the basin vary by only slightly more than one degree C. As a result, it is unlikely that corals in these two areas are adapted to completely different temperature regimes and consequently have significantly different tolerances to the same temperature range. We, therefore, rule temperature out as the dominant control on Caribbean coral growth and consider alternate parameters that may have an influence on growth rates in these two areas.

Western Caribbean Coral Growth & the Atlantic Multidecadal Oscillation

Coral growth for the Western Caribbean compilation, including records from the Yucatan, Belize and the Bahamas, exhibits a strong relationship with the Atlantic Multidecadal oscillation (AMO) for the period 1950-2010 (figure 33; Saenger et al., 2009, Vasquez-Bedoya et al., 2012). The AMO is the leading mode of Atlantic SST variability on decadal time scales and oscillates between periods of anomalously warm SST and periods of anomalously cool SST with a periodicity of about 50-90 years (Enfield et al., 2001). The AMO was predominantly in a negative phase during the period 1950-2000 with a shift towards positive AMO post 2000. Coral growth rates are *inversely* correlated with the AMO (figure 33, note that the coral growth axis is inversed), meaning that coral growth is highest during the prolonged period of negative AMO, when associated SSTs are coolest and lowest when the AMO shifts towards its positive phase, when associated SSTs are warmest. On inter-annual timescales, the AMO accounts for approximately 40% of the variability in coral growth ($r^2=0.39$) and 60% of the variability on 7-year timescales.

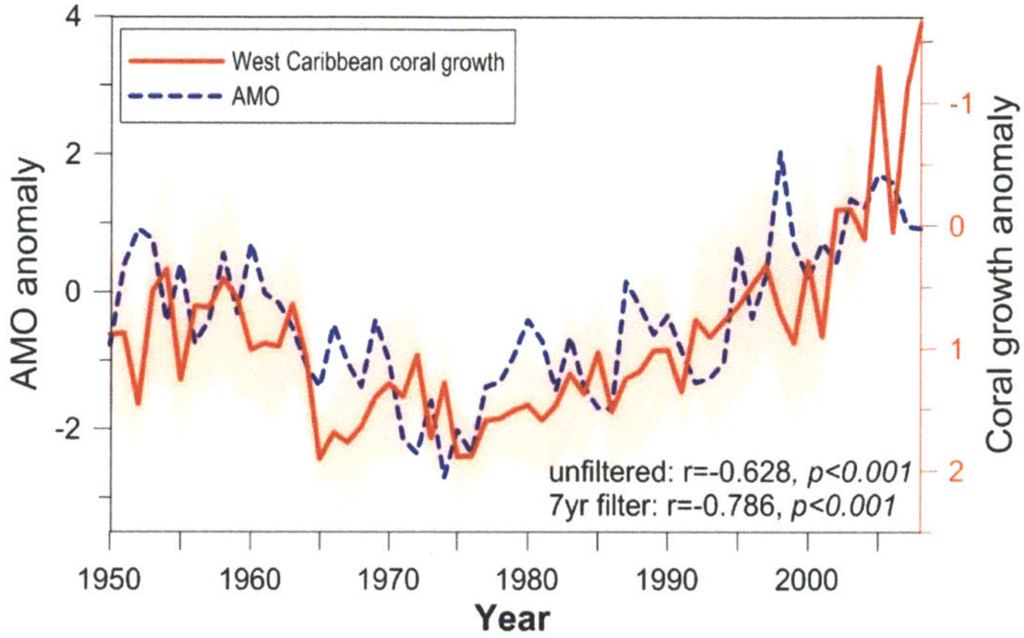

Figure 33. Relationship between West Caribbean coral growth (red line) and the Atlantic decadal oscillation (blue dotted line). The coral growth axis is reverse here to show the inverse correlation. Standard error associated with coral growth is depicted by the shaded red bar. R and p-values are given for the unfiltered records and for a 7-year filter.

Several previous studies have found relationships between coral growth in the Caribbean and the AMO, including a recent study by Vasquez-Bedoya et al. (2012; which includes some of the corals used in this study) who examined coral growth from 3 specimens of *Siderastrea siderea* from the Yucatan and found a significant, inverse relationship between the AMO and coral growth over the period 1860-2008. Hetzinger et al. (2008) describe a strong, consistent relationship between coral $\delta^{18}O$ - a function of SST and seawater $\delta^{18}O$ ($\delta^{18}O_{sw}$) - and AMO variability from 1918-2004 in a *Diploria strigosa* colony in the Los Roques archipelago, north of Venezuela, at the southern boundary of the Caribbean current. The AMO is thought to influence Atlantic hurricane activity (Goldenberg et al., 2001) which, in turn affects the $\delta^{18}O_{sw}$ and hence the $\delta^{18}O$ incorporated in to the coral skeleton. Hurricane activity increased, from the period 1971-1994 when there were an average of 1.5 major hurricanes per year to the period 1995-2005 when there were an average of 4.1 major hurricanes per year (Nyberg et al., 2007) coincident with the shift in the AMO from negative to positive. Although hurricane activity may have influenced the reef sites in the Western Caribbean to a certain degree it seems unlikely that the tight link between coral growth and the AMO is through periodic storm activity alone.

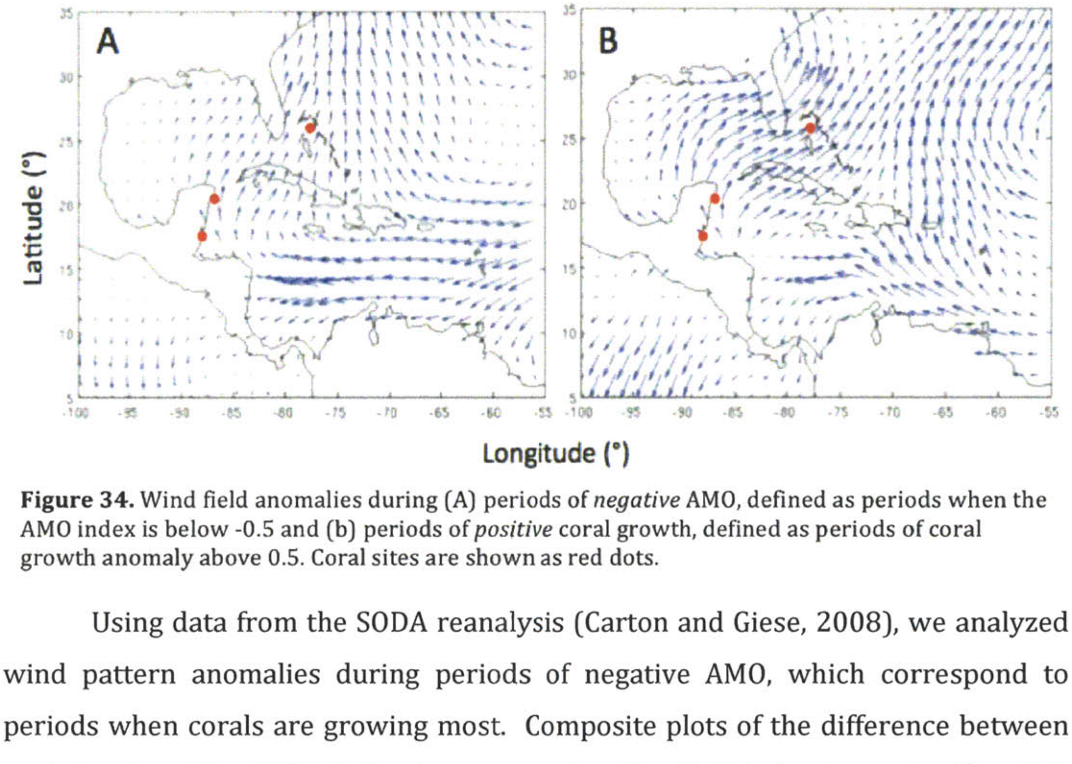

Figure 34. Wind field anomalies during (A) periods of *negative* AMO, defined as periods when the AMO index is below -0.5 and (b) periods of *positive* coral growth, defined as periods of coral growth anomaly above 0.5. Coral sites are shown as red dots.

Using data from the SODA reanalysis (Carton and Giese, 2008), we analyzed wind pattern anomalies during periods of negative AMO, which correspond to periods when corals are growing most. Composite plots of the difference between periods of positive AMO, defined as years when the AMO index is greater than 0.5, and periods of negative AMO, defined as years when the AMO index is less than -0.5 show that a positive AMO invokes a Southerly (South-North) wind direction in the Western Caribbean (figure 34a). Furthermore, there is a strong correlation between the AMO and wind strength off of the Yucatan Peninsula (figure 35). When we

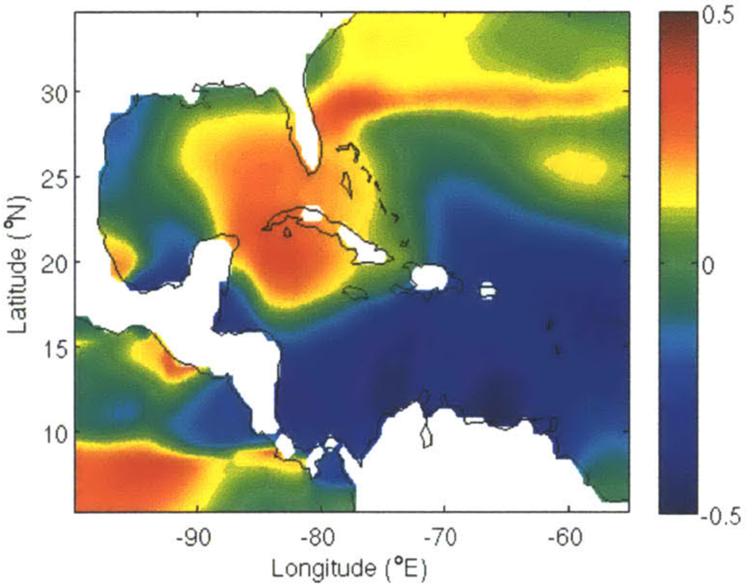

Figure 35. Correlation map of AMO and wind strength. The color bar represents r values for the correlation.

conducted a similar analysis of the wind patterns during periods of increased coral growth (>0.5), the same pattern emerged, with anomalously strong Southerly winds off the coast of the Yucatan. This implies that wind direction off the coast of the Yucatan has a strong influence on coral growth in the Western Caribbean To test this theory, an index of meridional wind strength in this area was constructed by averaging the meridional winds in a regional box off of the Yucatan (16-20°N, 84-87°W; figure 36). There is a high correlation between both AMO and coral growth with this index on inter-decadal and 7 year time scales (table 6). We hypothesize that the tight link between AMO and coral growth is due to the strong connection between the AMO and wind strength in this area (figure 35).

Table 6. Correlations between AMO and Coral growth with the Meridional wind index

	r	p
AMO	-0.361	<0.001
AMO (7yr Filter)	-0.555	<0.001
Coral Growth	0.356	<0.001
Coral Growth (7yr Filter)	0.543	<0.001

As current direction in the Caribbean is strongly influenced by the strength and direction of the wind (Gordon, 1967), we hypothesize that this anomalous

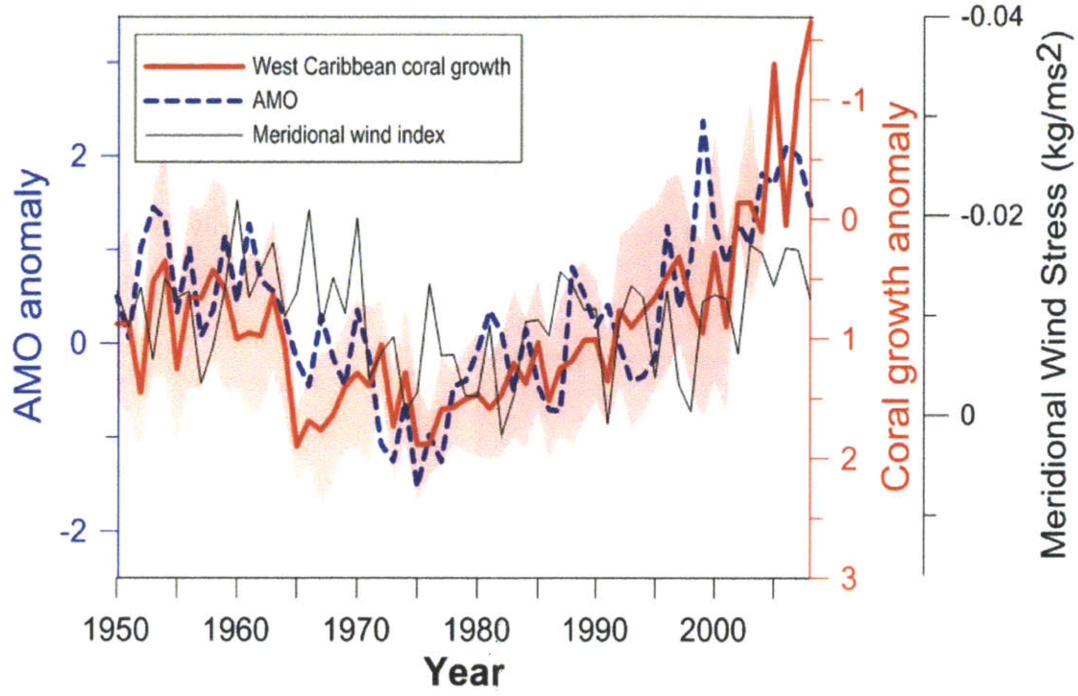

Figure 36. Relationship between West Caribbean coral growth (green line), the Atlantic Multidecadal Oscillation (blue dashed line) and the meridional wind index (black line), constructed by averaging the zonal wind in the area 16-20°N, 84-87°W. Standard error associated with coral growth is depicted by the shaded green bar.

meridional wind direction may affect the local currents, promoting Ekman transport off the coast of Central America (figure 37). In the Northern Hemisphere, Ekman transport occurs at 90° to the right of the direction of wind propagation (Knauss, 1997). This means that the net transport of water would be East-West off the coast of Central America promoting upwelling of nutrient rich water from depth, providing a potential mechanism to link the AMO and coral growth.

The same composite plots made for the currents in the Caribbean during negative AMO and positive coral growth, show a consistent strengthening of the Caribbean current (figure 38). The increase in the strength of the Caribbean current during periods of negative AMO and positive coral growth may increase the advection of nutrients to the western Caribbean making them more accessible to the reef sites.

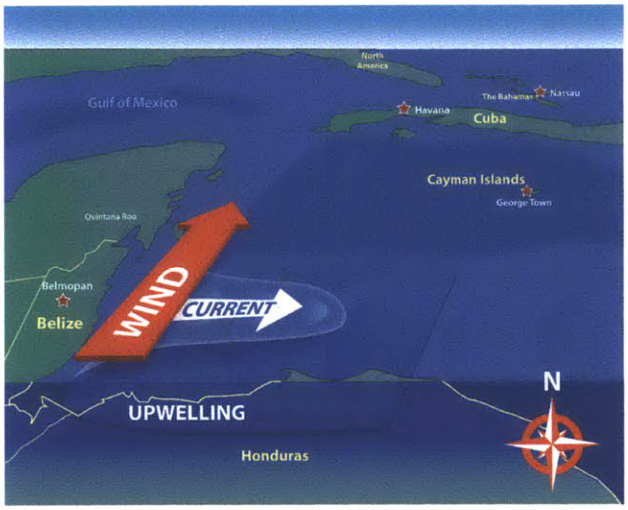

Figure 37. Graphic depicting the eastward current direction and upwelling associated with a Southerly wind direction off the coast of Belize and the Yucatan.

The relationship between coral and nutrient availability is complex; generally corals inhabit oligotrophic regions because these tend to be the areas where light availability is highest (Barnes, 1987); however, nutrients are essential to coral reef ecosystems as they promote primary productivity. As a result, corals can benefit from the addition of nutrients to the reef in two ways: (1) the added nutrients promote productivity on the reef resulting in an increase in the availability of material for heterotrophic feeding (2) the corals can benefit directly from the addition of nutrients. Corals require nutrients to survive and several studies have

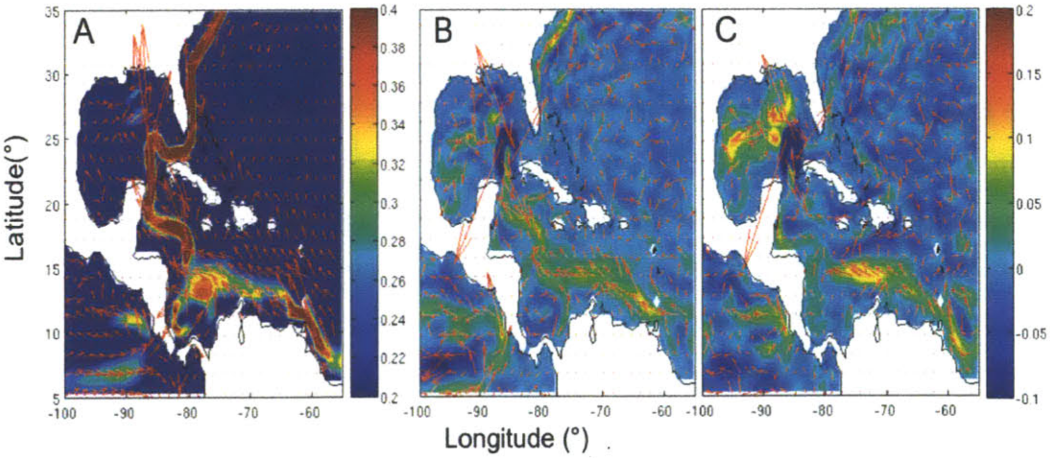

Figure 38. Maps of current speed (colors) and direction (red arrows). showing (A) averaged currents from 1950-2008, (B) current field anomalies during periods of *positive* AMO, defined as periods when the AMO index is below -0.5 and (C) periods of *positive* coral growth, defined as periods of coral growth anomaly above 0.5.

found that coral growth rates increase in the presence of key nutrients (Koop et al., 2001; Marubini and Thake 1999). Indeed, Dodge and Vaisnys (1975) found an inverse relationship between coral growth and air temperatures at Bermuda and attributed this inverse relationship to the inverse relationship between temperature and nutrient supply in Bermuda. Nutrients are supplied to Bermuda by the deep mixing of colder water and thus they are in greatest abundance when water temperatures are coldest (Menzel and Ryther, 1961). On the other hand, an overabundance of nutrients can lead to high macroalgal and phytoplankton growth rates which can then result in unfavorable conditions for skleractinian coral growth (Szmant-Froelich, 1983).

The effect of nutrients on coral growth is dependent on the concentration of nutrients and the duration of exposure. Corals can be exposed to nutrients in several different forms including particulate matter and dissolved inorganic and organic nutrients. As most organic nutrients such as nitrogen and phosphorus are rapidly assimilated by phytoplankton, normally only a small percentage of these nutrients are readily available for coral usage. Coral tissue thickness, which is linked to coral growth, has been shown to be related to the amount of nutrients with thicker tissues corresponding to more nutrient availability (Barnes and Lough, 1992; Lough and Barnes, 2000). In an *in situ* nutrient enrichment experiment on the GBR, Koop et al. (2001) found that coral linear extension and calcification increased with the addition of phosphorus. Likewise, Atkinson et al. (1995) reported that 57 coral species grew well in aquaria with high nutrients, supporting the conclusion of Smith and Buddemeier (1992) that coral growth rates are not necessarily negatively affected by moderately high nutrient concentrations.

Coral reefs are incredibly efficient at recycling nutrients but still require "new" nutrients to enter the system for net production or growth (Szmant-Froelich, 1983). New nutrients can enter the reef from either terrestrial run off (Marsh, 1977) or from oceanic sources. Generally, corals avoid areas of high runoff due to salinity stress, excessive nutrients and sedimentary output, which can reduce light availability. The oceanic sources of nutrients to the reef are dependent on (1) the concentration of nutrients in the reef source waters, (2) the rate of flow of water across the reef and (3) the ability of primary producers to take up the nutrients at a given concentration (Szmant-Froelich, 1983). Upwelling can increase the nutrient concentration of the source water (Thompson and Golding, 1981; Andrews and Gentien, 1982) and wave energy can increase the flow of these nutrients across the reef (Scoffin et al., 1992).

The flow of water across a reef, which is in part controlled by wind strength, is an important environmental variable influencing coral growth (Scoffin et al., 1992). Coral growth rates are enhanced by flow due to decreased sedimentation, increased photosynthetic and respiration rates, enhanced access to food and more efficient food particle capture. The relationship between AMO and wind stress in the Western Caribbean (figure 24) may also contribute to an increase in water motion across the reef during periods of negative AMO contributing to the observed increase in coral growth. Smith and Kinsey (1976) found that shallow coral reefs exposed to high energy environments produce roughly 5 times the amount of calcium carbonate per square meter than protected reef environments. Kuffner (2002) determined that corals transplanted to a high flow regime exhibited significantly higher rates of calcification than those transplanted to a low water motion regime. An *in situ* experiment on the growth of *Agaricia* under different flow environments showed that growth rates were higher in high flow environments than in low flow environments (Sebens et al., 2003).

In summary, coral growth rates in the Western Caribbean are highly correlated with and likely influenced by wind driven currents associated with the AMO, inducing either upwelling and advection of nutrients to the coral sites, or increasing the water flow across the reef. Growth rates in Bermuda appear to be directly affected by the upwelling of nutrient rich water, unrelated to changes in the AMO.

Eastern Caribbean Coral Growth & the Pacific Decadal Oscillation

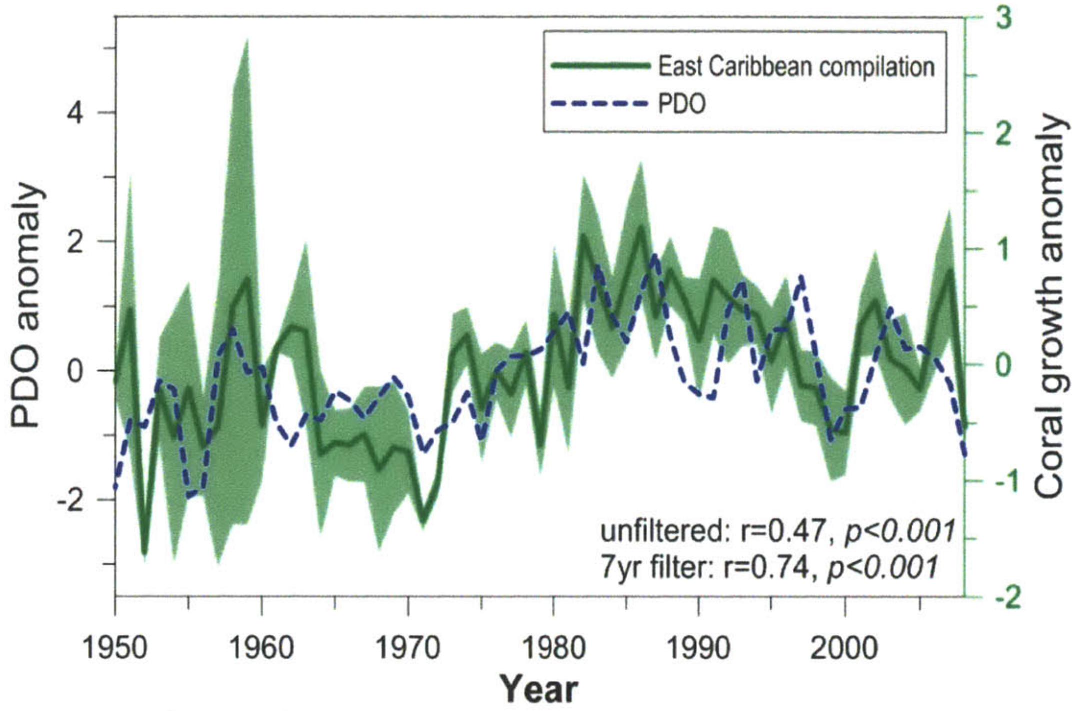

Figure 39. Relationship between East Caribbean coral growth (green line) and the Pacific Decadal Oscillation (blue dashed line). Standard error associated with coral growth is depicted by the shaded green bar. R and p-values are given for the unfiltered records and for 7-year filters.

Coral growth in the Eastern Caribbean, with the exception of the corals from Hans-Lolik, USVI closely tracks changes in the Pacific Decadal Oscillation (PDO) for the period 1950-2010 (figure 39). The PDO is the leading principal component of monthly SST anomalies in the North Pacific, pole-ward of 20°N (Mantua et al., 1997). It oscillates between a positive phase where SSTs in the Eastern basin are anomalously warm and SSTs in the Western basin are anomalously cool and a negative phase where SST's in the Eastern basin are anomalously cool and SSTs in the Western basin are anomalously warm. PDO has similar spatial SST characteristics to the El Niño-Southern Oscillation (ENSO) but operates on much longer, decadal timescales, oscillating between positive and negative phases approximately every 20-30 years.

Coral growth rates are positively correlated to the PDO, meaning that corals grow most in the Eastern Caribbean when PDO is in its positive phase, and least when PDO is in its negative phase. Variations in the PDO account for approximately 20% of coral growth on inter-annual timescales, and approximately 55% of coral growth on longer, 7-year time scales. While the PDO is predominantly a Pacific SST phenomenon it has large effects on Caribbean climate through atmospheric teleconnections. Periods of positive PDO are associated with increased frequency of El Niño like conditions in the Pacific region (Seager et al., 2009). El Niño affects Caribbean circulation by weakening the Caribbean Low Level Jet (CLLJ) and diminishing the propagation of Easterly tropical waves (Amador et al., 1998). Easterly tropical waves encourage the production of tropical cyclones (Landsea et al., 1998) and so bring increased rain to Mesoamerica and the Caribbean. As a result, positive (negative) PDO events are linked to prolonged dry (wet) periods (Méndez & Magaña, 2010). This is one mechanism through which the PDO could affect coral growth. Coral growth has been shown to be affected by light availability (Chalker et al., 1988) which is tightly linked to cloud cover and precipitation. An increase in light availability during prolonged droughts may lead to enhanced coral growth in

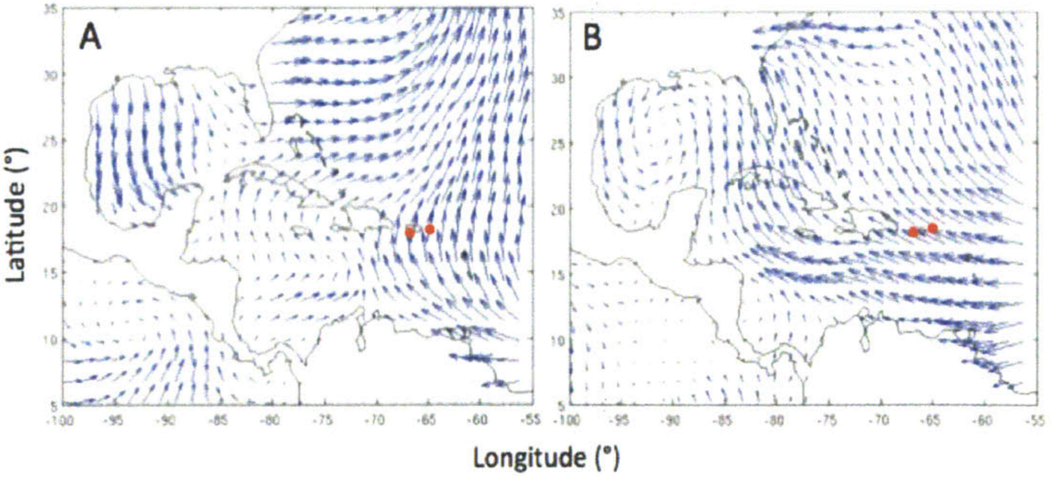

Figure 40. Wind field anomalies during (A) periods of *positive* PDO, defined as periods when the PDO index is above 0.5 and (B) periods of *positive* coral growth, defined as periods of coral growth anomaly above 0.5. Coral sites are shown as red dots.

the Eastern Caribbean but does not explain why coral growth is not concomitantly enhanced in the Western basin.

We find that the PDO also has an effect on the direction and strength of wind in the Eastern Caribbean (figures 40,41). Composite plots of the difference between periods of positive PDO, defined as years when the PDO index is greater than 0.5, and periods of negative PDO, defined as years when the PDO index is less than 0.5, show that the winds are strengthened during positive PDO events and exhibit a slight Southeasterly tilt (ie. SE-NW direction) in the Southeastern Caribbean off the coast of South America (figure 40a). In addition, there is a high correlation between the PDO and wind strength in this area (figure 41). A similar analysis of the wind field anomalies during periods of positive coral growth indicate that corals grow most when the trade winds are strongest off of South America (figure 40b). In order to assess the relationship between PDO, Eastern Caribbean coral growth and the zonal winds off of south America, an index of zonal wind strength in this area was constructed by averaging the zonal winds in a regional box off of South America (6-8°N, 55-57°W; figure 42). There is a high correlation between both PDO and coral growth with this index (table 7). Because the northward surface currents in the tropical Atlantic are primarily driven by Ekman dynamics with the meridional transport of water being proportional to the zonal

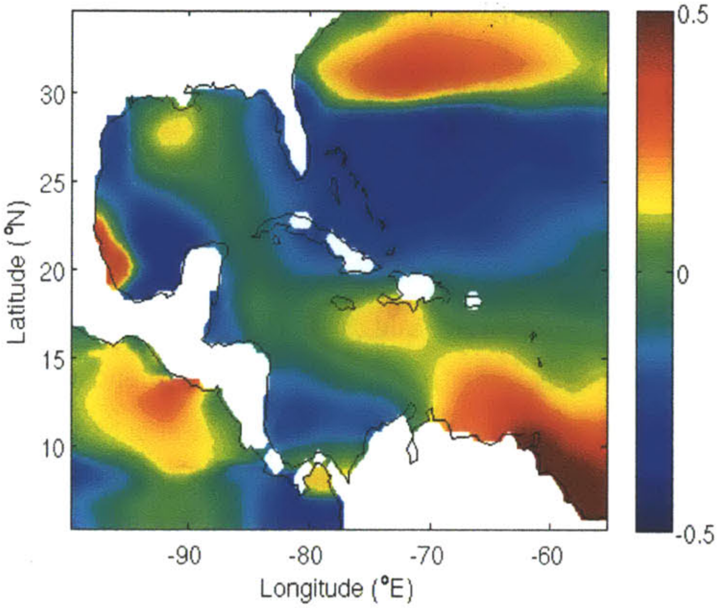

Figure 41. Correlation map of PDO and wind strength. The color bar represents r values for the correlation.

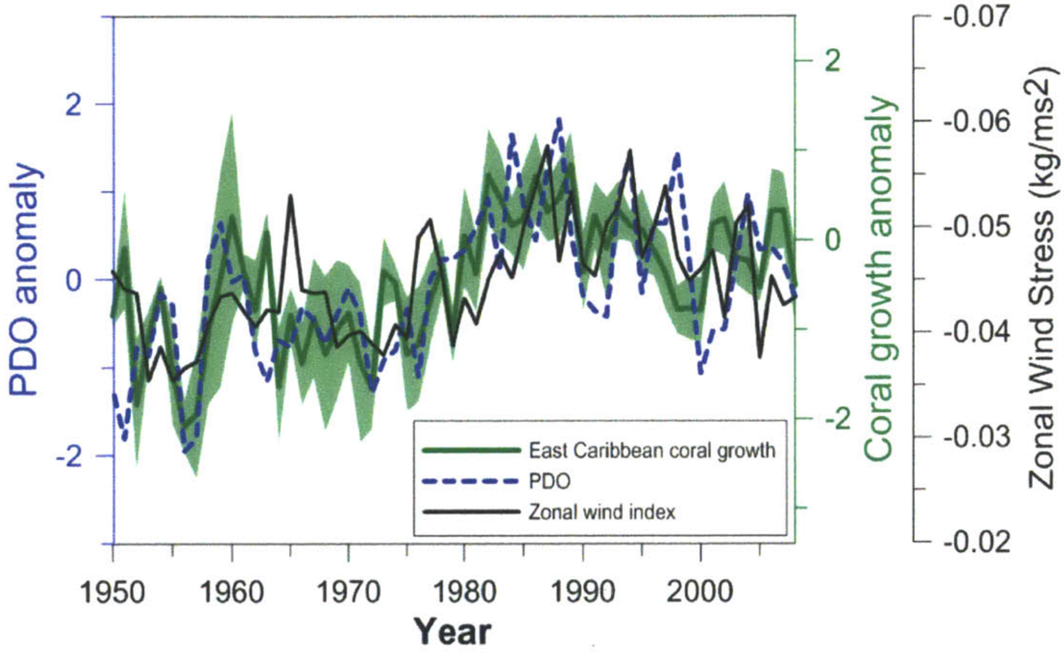

Figure 42. Relationship between East Caribbean coral growth (green line), the Pacific Decadal Oscillation (blue dashed line) and the zonal wind index (black line), constructed by averaging the zonal wind in the area 6-8°N, 55-57°W. Standard error associated with coral growth is depicted by the shaded green bar.

wind stress (Mayer and Weisberg, 1993) the winds in this area have an important impact on the circulation of water to the Eastern Caribbean. Kilbourne et al. (2008) noted that the strength of the easterly wind component in the northern tropics increased post 1970, which would lead to an increase in the northward Ekman transport. This shift is coincident with the transition of the PDO from negative to positive.

Table 7. Correlations between PDO and Coral growth with the zonal wind index

	r	p
PDO	-0.497	<0.001
PDO (7yr Filter)	-0.684	<0.001
Coral Growth	-0.485	<0.001
Coral Growth (7yr Filter)	-0.793	<0.001

The same composite plots made for the currents in the Caribbean during positive PDO and positive coral growth do not show coherent patterns in the Eastern part of the basin (figure 39). This is most likely due to the limited instances during which PDO and coral growth are positive over the 1950-2010 time period resulting in current maps which are heavily influenced by random eddy activity. This is due in part to the highly variable nature of currents in the Caribbean (Centurioni and Niiler, 2003) and to limitations in the SODA reanalysis current product.

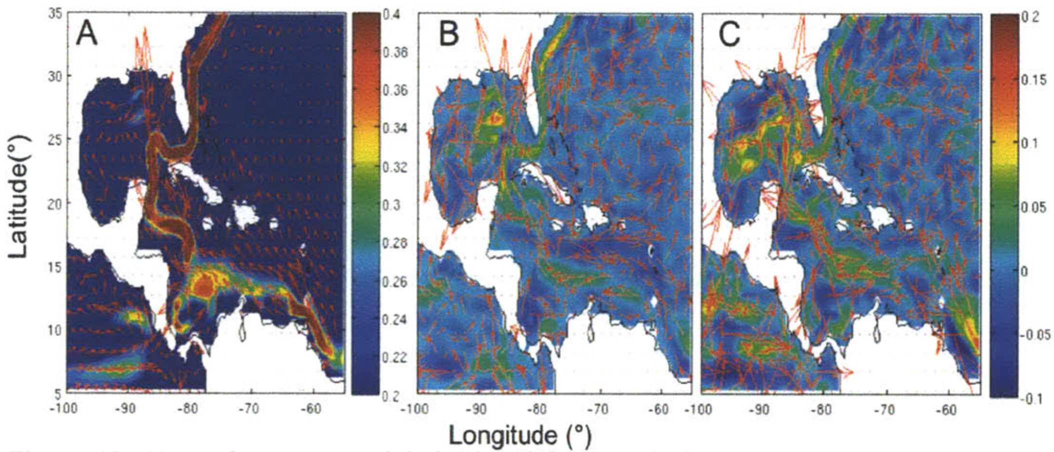

Figure 43. Maps of current speed (colors) and direction (red arrows). showing (A) averaged currents from 1950-2008, (B) current field anomalies during periods of *negative* PDO, defined as periods when the PDO index is below -0.5 and (C) periods of *positive* coral growth, defined as periods of coral growth anomaly above 0.5.

There are two ways in which the effect of the PDO on wind strength off of South America would bring nutrients to the coral sites on the southern side of the islands of Puerto Rico and the UVSI, (1) through increased upwelling off the coast of South America and advection of this nutrient rich water to the Eastern Caribbean, (2) through the increased advection of nutrient-rich southern source water. In the Cariaco Basin, an increase in trade wind strength promotes upwelling from November to May of each year. The winds off the coastal ocean result in the rising of isotherms, bringing nutrient-rich subsurface waters to the surface and inducing an increase in primary production in the surface layer as well as an increase in the concentration of chlorophyll-a (Alvera-Azcarate et al., 2010). It is well established through records of salinity, chlorophyll and colored dissolved organic material (CDOM) that water from off the coast of South America is advected towards the islands of Puerto Rico and the USVI (Kilbourne et al., 2008). Much of the Caribbean Sea, including the area directly south of the Northern-most Lesser Antilles is affected by runoff from the Orinoco and Amazon rivers year round (Froelich et al., 1978; Corredor and Morell, 2001; Hu et al., 2004). The advection of this water brings with it higher nutrient concentrations and organic material which can promote primary productivity on the reef sites (see section on nutrients above).

Another source of nutrients to the southern side of the Lesser Antilles is through the advection of nutrient-rich southern source water. The nutrients in the Antilles current and the Caribbean current, which ultimately feed the Gulf Stream originate from Sub-Antarctic Mode Water and Antarctic Intermediate water formed in the Southern Ocean (Sarmiento et al., 2004; Williams et al., 2006). These nutrient rich waters may be upwelled off the coast of South America and advected to the coral sites, or alternatively they may be upwelled directly at the coral sites.

The anomalous records from Hans-Lolik that do not follow variations in the PDO are likely to be instead influenced by a different environmental regime. While they are positively correlated to SSTs from the Atlantic, the relationship is insignificant for the period 1950-2009. North of Puerto Rico and the USVI, salinities are substantially higher than on the southern shores of these islands, indicating that they are located at the very tip of the influence of tropical precipitation and runoff (Corredor and Morrell, 2001). Instead, the Northern side of the islands are likely to be much more strongly influenced by changes in the tropical Atlantic. If nutrient advection and/or flow also play a dominant role in the growth of these coral records, it is probable that coral growth is linked to processes in the Atlantic which would advect nutrients to this site, such as ocean eddies and nutrients from the subtropical gyre. Indeed, maps of the distribution of nutrients in the North Atlantic (Torres-Valdés et al., 2009) show a distinct boundary between nutrient concentrations south of the Lesser Antilles and north of the Lesser Antilles, suggesting that the environmental conditions for coral growth on either side of these islands may be quite different.

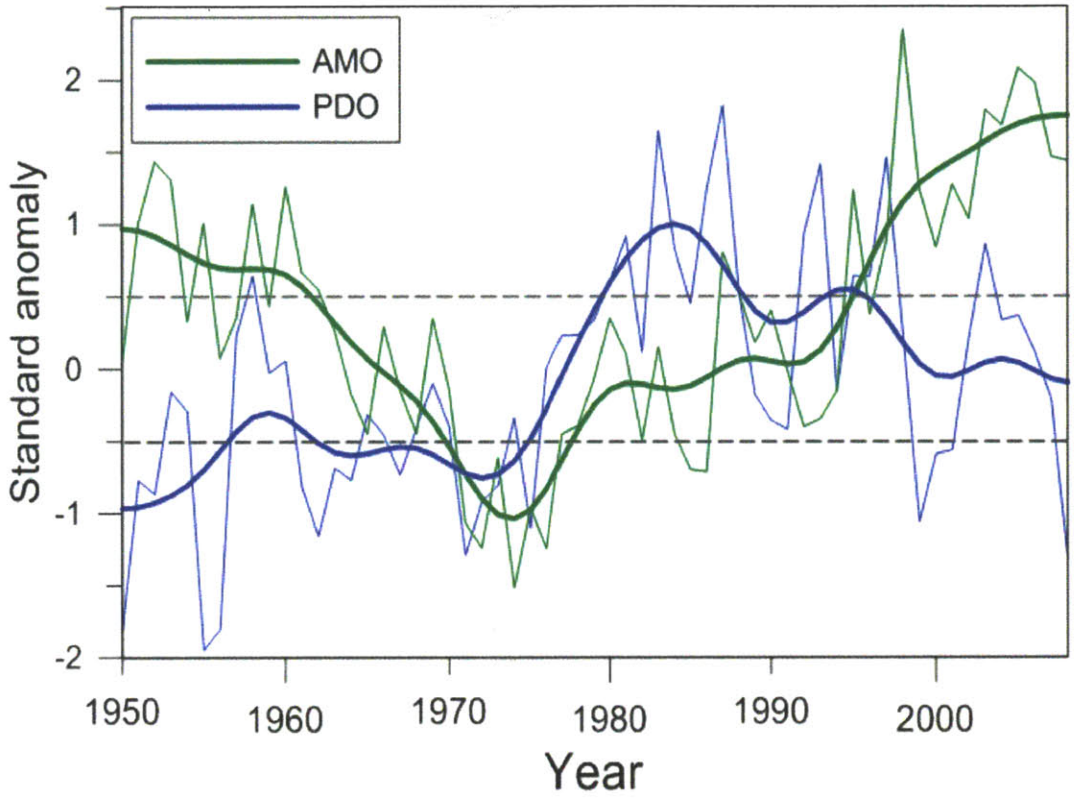

Figure 40. Time series of the AMO (green) and PDO (blue). Thin lines indicate inter-annual variations, thick lines denote a 10year Gaussian filter. Dashed gray lines depict the thresholds for "positive" and "negative" events used to construct the composites.

The question still remains as to why corals in the Eastern Caribbean respond to changes in the PDO while corals in the Western Caribbean respond to the AMO. It is clear from figure 40 that during the period 1950-2010, the AMO and the PDO are rarely in phase and that the wind composites constructed for each mode are representative of different periods. It is thus, unsurprising that the wind field anomalies are so different for the AMO and the PDO. One reason why Eastern Caribbean coral growth may respond to the PDO while west Caribbean coral growth does not is that the effect of the PDO on wind strength and direction in the

Caribbean seems to be greatest in the Eastern part of the basin. Conversely, the wind field anomaly associated with AMO in the eastern part of the basin does not vary much from the long-term mean wind field (see figure 24, part I). It appears that, unlike the PDO, the winds associated with the AMO do not promote anomalous conditions conducive for upwelling and advection of nutrient rich waters to Puerto Rico and the USVI. Likewise, the PDO does not seem to affect the winds sufficiently in the western basin to have an effect on coral growth in this area.

In this era of rapid environmental change, coral growth records are essential to understanding the link between coral growth and environmental parameters. It is clear that corals in different regions are susceptible to a variety of different stressors and factors that influence the extent of their annual growth. The ability of corals to successfully extend their skeletons annually is an important factor governing their ability to withstand extreme environmental stressors (Hoegh-Guldberg et al., 2007). A clear understanding of the underlying factors governing this growth is, therefore, essential to understanding their susceptibility to more transient events associated with global warming such as thermal stress and hurricane activity. Climate change is predicted to have significant effects on modes of climate variability in the future (IPCC AR4, 2007), but global climate model simulations to date have failed to predict the amplitude and timing of future oscillations in either the PDO or the AMO. As these modes of climate variability and their impact on wind stress seem to play an important role in coral growth across the Caribbean, future efforts should focus on (1) the trajectory of these modes in the future and (2) the relationship between these modes and future coral growth.

Conclusions

1) The relationship between coral growth and SST varies spatially in the Caribbean basin.

2) Coral growth rates in the Western Caribbean (Yucatan, Belize and Bahamas) are strongly *inversely* correlated to the Atlantic Multidecadal Oscillation and, by proxy, regional SST.

3) The coral growth rate compilation for corals from the southern side of the islands of Puerto Rico and the USVI are significantly *positively* correlated to the Pacific Decadal Oscillation.

4) Corals on the northern side of the USVI have a *positive* relationship with Atlantic SST and are likely influenced by nutrient advection through the subtropical gyre and/or Atlantic eddies.

5) Wind driven circulation in the Caribbean appears to have a significant effect on coral growth either through the advection of nutrients to coral sites, or through flow dynamics on the reef.

6) The future trajectories of the AMO and PDO in response to climate change may have important implications for the ability of corals in the Caribbean to withstand extreme episodic events.

5. References

Alvarez-Filip, L., Gill, J.A., Dulby, N.K., Perry, A.L., Watkinson, A.R., and I.M. Côté (2011) Drivers of region-wide declines in architectural complexity on Caribbean reefs. *Coral Reefs* **30**, 1051-1060

Alvera-Azcárate, A., Barth, A. and R.H. Weisberg (2009) The Surface Circulation of the Caribbean Sea and Gulf of Mexico as Inferred from Satellite Altimetry. *Journal of Physical Oceanography* **39**, 640-657

Amador, J.A. (1998) A Climatic Feature of the Tropical Americas: The Trade Wind Easterly Jet. *Topicos Meteorologicos Oceanograficos* **5** (2), 91-102

Andrews, J.C. and P. Gentien (1982) Upwelling as a source of nutrients for the Great Barrier Reef ecosystems – a solution to the Darwin Question. *Marine Ecology – Progress Series* **8** (3), 257-269.

Atkinson, M.J., B. Carlson, and G.L. Crow (1995) Coral growth in high-nutrient, low-pH seawater. A case study of corals cultured at the Waikiki Aquarium, Honolulu, Hawaii. *Coral Reefs* **14** (4), 215-223.

Bak, R.P.M., Nieuwland, G., and E.H. Meesters (2009) Coral growth rates revisited after 31 years: what is causing lower extension rates in *Acropora palmata*? *Bulletin of Marine Science* **84**, 287–294.

Barnes, D.J., and J.M. Lough. 1993. On the nature and causes of density banding in massive coral skeletons. *Journal of Experimental Marine Biology and Ecology* **167**,91–108,

Barnes, D.J., and J.M. Lough. 1999. Porites growth characteristics in a changed environment: Misima Island, Papua New Guinea. *Coral Reefs* **18**(3):213–218

Bessat, F. & Buigues, D. (2001) Two centuries of variation in coral growth in a massive *Porites* colony from Moorea (French Polynesia): a response of ocean-atmosphere variability from south central Pacific. *Palaeogeography Palaeoclimatology Palaeoecology* **175,** 381–392

Bates, N.R., Amat, A., Andersson, A.J., (2010) Feedbacks and responses of coral calcification on the Bermuda reef system to seasonal changes in biological processes and ocean acidification. *Biogeosciences* **7**, 2509–2530.

Bjerknes, J. (1969) Atmospheric teleconnections from the equatorial. Pacific, *Monthly. Weather. Rev.* **97**,163 - 172.

Bonilla, J., W. Senior, J. Bugden, O. Zafiriou, and R. Jones (1993) Seasonal Distribution of Nutrients and Primary Productivity on the Eastern Continental Shelf of Venezuela as Influenced by the Orinoco River. *Journal of Geophysical Research* **98**, 2245-2257

Bruckner, A. (2002). Life-Saving Products from Coral Reefs. *Issues in Science and Technology*. Spring Ed.

Bruckner, A. & Hill, R., (2009) Ten years of change to coral communities off Mona and Desecheo Islands, Puerto Rico, from disease and bleaching. *Diseases of Aquatic Organisms* **87**, pp.19–31.

Bryant, D.L., Burke, D.L., Mc Manus, J., Spalding, M. (1998) Reefs at Risk: A Map-

Based Indicator of Threats to the World's Coral Reefs (World Resources Institute, Washington, DC)

Buddemeier, R.W., Lane, D.R. and J.A. Martinich (2011) Modeling regional coral reef responses to global warming and changes in ocean chemistry: Caribbean case study. *Climate Change* **109**, 375-397

Burke, L., Bryant, D., McManus, J., and Spalding, (1998) M. Reefs at Risk. World Resources Institute (WRI): 56 p.

Burke, L., Selig, L. and Spalding, M. (2002) Reefs at risk in Southeast Asia. World resources institute, in: Commission on the measurement of economic performance and Social progress 2009, (ed.), *Provisional summary of the commission's work - Working Papers and Reports*. Washington. Available at http://www.stiglitz-sen-fitoussi.fr/en/index.htm (last access 20 August 2009).

Burke, L., and J. Maidens (2004) Reefs at Risk in the Caribbean. World Resources Institute, Washington, DC.

Cantin, N.E., A.L. Cohen, K.B. Karnauskas, A.M. Tarrant and D.C. McCorkle (2010) Ocean Warming Slows Coral Growth in the Central Red Sea. *Science* **329**, 322-329

Carton, J.A., G. Chepurin, and X. Cao (2000) A Simple Ocean Data Assimilation analysis of the global upper ocean 1950-1995 Part 2: results, *Journal of Physical Oceanography*, **30**, 311-326.

Carton, J. A. and B. S. Giese, 2008: A Reanalysis of Ocean Climate Using Simple Ocean Data Assimilation (SODA), *Mon. Weather Rev.*, **136**, 2999-3017

Carricart-Ganivet JP, Merino M (2001) Growth responses of the reef building coral *Montastraea annularis* along a gradient of continental influence in the southern Gulf of Mexico. *Bulletin of Marine Science* **68**.

Carricart-Ganivet J (2004) Sea surface temperature and the growth of the West Atlantic reef-building coral *Montastraea annularis. Journal of Experimental Marine Biology and Ecology* **302**, 249-260.

Carricart-Ganivet, J.P., (2007) Annual density banding in massive coral skeletons: result of growth strategies to inhabit reefs with high microborers' activity? *Marine biology* **153**(1), pp.1-5.

Castillo, K.D., Ries, J.B., and J.M. Weiss (2011) Declining coral skeletal extension for forefeef colonies of *Siderastrea siderea* on the Mesoamerican Barrier Reef system, southern Belize. *PLoS One* **6**, e14615.

Castillo, K.D., J.B. Ries, J.M. Weiss and F.P. Lima (2012) Decline of forereef corals in response to recent warming linked to history of thermal exposure. *Nature Climate Change* **2**, 756-760.

Centurioni, L.R. and P.P. Niiler, (2003) On the surface currents of the Caribbean Sea. *Geophysical Research. Letters* **30**, No. 6

Chalker, B.E., D.J, Barnes, W.C. Dunlap, et al. (1988) Light and Reef Building corals. *Interdisciplinary Science Reviews* **13** (3), 222-237

Chatfield, C. (1996) The analysis of time series: an introduction. Chapman & Hall, London, UK

Clausen, C.D. & Roth, A.A., (1975) Effect of Temperature and Temperature Adaptation on Calcification Rate in the Hermatypic Coral *Pocillopora damicomis. Marine Biology*, pp.93–100.

Coles, P.L. Jokiel and C.R. Lewis (1976) Thermal tolerance in tropical versus subtropical Pacific reef corals. *Pacif. Sci.* ***30***, 159-166

Coles, S.L. and P.L. Jokiel (1978) Synergistic Effects of Temperature, Salinity and Light on the Hermatypic Coral *Montipora verrucosa . Marine Biology* **195**, 187–195.

Cooper, E., Burke, L., Blood, N. (2009) "Coastal Capital: Belize. The Economic Contribution of Belize's Boral Reefs and Mangroves." WRI Working Paper. World Resources Institute, Washington DC.

Cooper, T.F.De 'Ath, G., Fabricius, K.E., Lough, J.M. (2008) Declining coral calcification in massive Porites in two nearshore regions of the northern Great Barrier Reef. *Global Change Biology* **14**, 529-538

Corredor, J. E., and J. M. Morell (2001), Seasonal variation of physical and biogeochemical features in eastern Caribbean Surface Water. *Journal of Geophysical Research* **106**, 4517–4525,

Cruz Piñón, G., Carricart Ganivet, J.P. & Espinoza Avalos, J., (2003) Monthly skeletal extension rates of the hermatypic corals Montastraea annularis and Montastraea faveolata: biological and environmental controls. *Marine biology* **143**(3), 491–500.

De'ath, G., Lough, J.M., Fabricius, K.E. (2009) Declining Coral Calcification on the Great Barrier Reef. *Science* **323**, 116-119.

Davalos-Dehullu, E., Hernandez-Arana, H., Carricart-Ganivet, J.P., (2008) On the causes of density banding in skeletons of corals of the genus *Montastraea. Journal of Experimental Marine Biology and Ecology* **365**, 142–147.

Donner, S.D., Knutson, T.R., and M. Oppenheimer. (2007) Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. *Proceedings of the National Academy of Sciences of the United States of America* **104** (13)

Dodge, R.E., and J.R. Vaisnys, (1975) Hermatypic coral growth as environmental recorder. *Nature* **258**, 706–708.

Dodge R.E., and J.R. Vaisnys (1980) Skeletal growth chronologies of recent and fossil corals. In: Rhoads DC, Lutz RA (eds) Skeletal growth of aquatic organisms. Plenum, New York, pp 228-240

Dodge, R.E. (1981) Growth characteristics of reef-building corals within and external to a naval ordnance range: Vieques, Puerto Rico. In: Gomez, E.D., Birkeland, C.E., Buddemeier, R.W., Johannes, R.E., Marsh, J.A., Tsuda, R.T. (Eds.), *Proceedings of the 4th International Coral Reef Symposium., Manila, Philippines* **2**, pp. 241–248

Dodge, R.E. and J.C. Lang (1983) Environmental Correlates of Hermatypic Coral (Montastrea annularis) Growth on the East Flower Gardens Bank, Northwest Gulf of Mexico. *Limnology and Oceanography* **28**, 228-240

Dodge, R.E. and G. W. Brass. (1984) Skeletal extension, density, and calcification of a reef coral (*Montastrea annularis*): St. Croix, U.S. Virgin Islands. *Bulletin of Marine Science*

Dunbar, R.B., G.M. Wellington, M.W. Colgan, and P.W. Glynn (1994) Eastern Pacific sea surface temperature since 1600 A.D.: the delta ^{18}O record of climate variability in Galapagos corals. *Paleoceanography* **9**, 291–315.

Elizalde-Rendon, E.M. et al., (2010) Growth characteristics of the reef-building coral Porites astreoides under different environmental conditions in the Western Atlantic. *Coral Reefs* **29**(3), 607–614.

Enfield D.B (1996) Relationships of inter-American rainfall to tropical Atlantic and Pacific SST variability. *Geophysical Research Letters* **23**, 3305–3308.

Enfield D.B., and E.J. Alfaro (1999) The dependence of Caribbean rainfall on the interaction of the tropical Atlantic and Pacific Oceans. *Journal of Climate* **12**, 2093–2103.

Enfield D.B., A.M. Mestas-Nunez and P.J. Trimble (2001) The Atlantic Multidecadal Oscillation and its relation to rainfall and river flows in the continental US. *Geophysical Research Letters* **28** (10), 2077-2080.

Foster, A.B. (1980) Environmental variation in skeletal morphology within the Caribbean reef corals *Montastrea annularis* and *Siderastrea siderea*. *Bulletin of Marine Science* **30** (3), 678-709.

Fritts, H.C. (1976) Tree Rings and Climate. Academic Press Inc. London, UK

Froelich, P. N., Jr., D. K. Atwood, and G. S. Giese (1978), Influence of Amazon River discharge on surface salinity and dissolved silicate concentration in the Caribbean Sea, *Deep Sea Research* **25**, 735–744.

Gardner, T.A., Cote, I.M., Gill, J.A., Grant, A., Watkinson, A.R. (2003) Long-Term Region-Wide Declines in Caribbean Corals. *Science* **301**, 958-960

Glynn, P.W., Wellington, G.M., (1983) Coral Growth. In: Glynn, P.W., Wellington, G.M. (Eds.), Corals and Coral Reefs of the Galapagos Islands. University of California Press, pp. 93–118.

Goldenberg, S. B.; *et al.* (2001) The recent increase in Atlantic hurricane activity: Causes and implications. *Science* **293**: 474–479

Gordon, A.L., (1967) Circulation of the Caribbean Sea. *Journal of Geophysical Research*. **72**, 6207-6223.

Guzman, H.M., Cipriani, R., Jackson, J.J.B., (2008) Historical decline in coral reef growth after the Panama Canal. *Ambio* **37**, 342–346.

Grottoli A.G. (2001) Past Climate from Corals. *Encyclopedia of Ocean Sciences* [Eds. J Steele, S Thorpe, K Turekian], Academic Press, London pp. 2098-2107

Helmle, K.P., Dodge, R.E., Swart, P.K., Gledhill, D.K. and C.M. Eakin (2011) Growth rates of Florida corals from 1937 to 1996 and their response to climate change. *Nature Communication* **2**, 215.

Hetzinger, S., M. Pfeiffer, W.C. Dullo, N. Keenlyside, M. Latif and J. Zinke (2008) Caribbean coral tracks Atlantic Multidecadal Oscillation and past hurricane activity. *Geology* **36** (1), 11–14.

Highsmith RC (1979) Coral growth rates and environmental control of density banding. *Journal of Experimental Marine Biology and Ecology* **37**,105-125

Hoegh-Guldberg, O. (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* ***50*** (8), 839–866.

Hoegh-Guldberg, O., P. J Mumby, A. J Hooten, R. S Steneck, P. Greenfield, E. Gomez, C. D Harvell, et al. (2007) Coral Reefs Under Rapid Climate Change and Ocean Acidification. *Science* **318** (5857).

Hu, C., E. T. Montgomery, R. W. Schmitt, and F. E. Muller-Karger (2004), The dispersal of the Amazon and Orinoco river water in the tropical Atlantic and Caribbean Sea: Observation from space and S-PALACE floats, *Deep Sea Research Part II* **51**, 1151- 1171.

Hudson, J.H. (1981) Growth Rates in *Montastraea Annularis*: A Record of Environmental Change in Key Largo Coral Reef Marine Sanctuary, Florida. *Bulletin of Marine Science* **31**, 444-459

Hudson, J.H., Robbin, D.M., (1981) Effects of drilling mud on the growth rate of the reef building coral, *Montastraea annularis.* In: Geyer, R.A. (Ed.), Marine Environmental Pollution: Elsevier Oceanography Series, 27A, pp. 455–470.

Hudson, J.H., (1985) Long-term growth rates of Porites lutea before and after nuclear testing: Enewetak Atoll (Marshall Islands). In: Gabrie, C., Harmelin, M. (Eds.), *Proc. 5th Int. Coral Reef Congress*, Tahiti, 6, pp. 179–185.

Hughes, T (1994) Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. *Science* **265**, 1547-1551

Hughes, T.P. & Connell, J.H., (1999) Multiple stressors on coral reefs: A long-term perspective. *Limnology and oceanography* **44**(3), pp.932–940.

Hughes, T. P, A. H Baird, D. R Bellwood, M. Card, S. R Connolly, C. Folke, R. Grosberg, et al. (2003) Climate Change, Human Impacts, and the Resilience of Coral Reefs. *Science* **301** (5635).

Hurrell, J.W. and C. Deser (2009) North Atlantic climate variability: The role of the North Atlantic Oscillation. *Journal of Marine Systems* **78** (1), 28-41.

Johns, W.E., T.L. Townsend, D.M. Fratantoni and W.D. Wilson (2002) On the Atlantic inflow to the Caribbean Sea. *Deep Sea Research Letters* **49**, 211-243.

Jokiel, P.L. & Coles, S.L., (1977) Effects of temperature on the mortality and growth of Hawaiian reef corals. *Marine Biology* **43**(3), pp.201–208.

Jokiel, P.L. & Coles, S.L., (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* **8**(4), pp.155–162.

Kaplan, A. (2011) [Appendix E] Patterns and Indices of Climate Variability [in State of the Climate in 2010]. *Bulletin of the American Meteorological Society* **92** (6), S20-S25

Kilbourne, K.H., T.M. Quinn, R. Webb, *et al.* (2008) Paleoclimate proxy perspective on Caribbean climate since the year 1751: Evidence of cooler temperatures and multidecadal variability. *Paleoceanography* **23** (3)

Klein, S.A., B.J. Soden and N.C. Lau (1999) Remote sea surface temperature variations during ENSO: Evidence for a tropical atmospheric bridge. *Journal of*

Climate **12** (4), 917-932.

Knauss, J.A. (1997) Introduction to Physical Oceanography. Waveland Press Inc, Long Grove, IL

Knutson D, Buddemeier RW, Smith SV (1972) Coral chronometers: seasonal growth bands in reef corals. *Science* **177**, 270–272.

Koop, K. *et al.* (2001) ENCORE: The Effect of Nutrient Enrichment on Coral Reefs. Synthesis of Results and Conclusions. *Marine Pollution Bulletin* **42** (2), 91-120

Kuffner, I.B. (2002) Effects of ultraviolet radiation and water motion on the reef coral, *Porites compressa* Dana: a transplantation experiment. *Journal of Experimental Biology and Ecology* **270**:147-169.

Landsea, C. W., G. D. Bell, W. M. Gray, and S. B. Goldenberg (1998) The extremely active 1995 Atlantic hurricane season: Environmental conditions and verification of seasonal forecasts. *Monthly Weather Reviews* **126**, 1174–1193

Lee, T.N., W.E. Johns, R.J. Zantopp and E.R. Fillenbaum, (1996) Moored observartions of western boundary current variability and thermohaline circulation at 26.5°N in the subtropical North Atlantic. *Journal of Physical Oceanography* **26**, 962-983.

Lough, J.M. and D.J. Barnes (1997) Several centuries of variation in skeletal extension, density and calcification in massive *Porites* colonies from the Great Barrier Reef: a proxy for seawater temperature and a background of variability against which to identify unnatural change. *Journal of Experimental Marine Biology and Ecology* **211**, 29–67

Lough, J.M. and D.J. Barnes (2000) Environmental controls on growth of the massive coral *Porites*. *Journal of Experimental Marine Biology and Ecology* **245**, 225–243.

Lough, J.M. and T.F. Cooper (2011) New insights from coral growth band studies in an era of rapid environmental change. *Earth Science Reviews* **108**, 170-184

Jochum, M. and P.M. Malanotte-Rizzoli (2001) Influence of the Meridional Ocerturning Circulation on Tropical-Subtropical Pathways. *American Meteorological Society*, 1313-1323.

Joyce, T.M., A. Hernandez-Guerra, and W.M. Smethie, (2001) Zonal circulation in the northwest Atlantic and Caribbean from a meridional World Ocean Circulation Experiment hydrographic section at 66°W. *Journal of Geophysical Research* **106**, 22,095-22,113.

Maina, J. et al., (2011) Global Gradients of Coral Exposure to Environmental Stresses and Implications for Local Management D. Steinke, ed. *PLoS ONE* **6**(8), p.e23064.

Mantua, N.J., S.R. Hare, and Y. Zhang et al. (1997) A Pacific interdecadal oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* **78** (6), 1069-1079.

Mantua, N. and S.R. Hare (2002) The Pacific Decadal Oscillation. *Journal of Oceanography* **58** (1), 45-44

Manzello, D.P., (2010) Coral growth with thermal stress and ocean acidification:

lessons from the eastern tropical Pacific. *Coral Reefs* **29**, 749–758.

Marsh, J.A. (1977) Terrestrial inputs of nitrogen and phosphorus on fringing reefs of Guam. *138 Proc. Third Int. Coral Reef Symp,* Miami 1:331-336.

Marshall, J., Y. Kushnir, D. Battisti, P. Chang, A. Czaja, R. Dickson, J. Hurrell, M. McCartney, R. Saravanan and M. Visbeck (2001) North Atlantic Climate Variability: Phenomena, Impacts and Mechanisms. *International Journal of Climatology* **21**, 1863-1898

Marshall, A. T. & Clode, P., (2004) Calcification rate and the effect of temperature in a zooxanthellate and an azooxanthellate scleractinian reef coral. *Coral Reefs* **23**(2), 218–224.

Marubini, F. and B. Thake (1999) Bicarbonate Addition Promotes Coral Growth. *Limnology and Oceanography* **44** (3) 716-720.

Mayer, D.A., and R.H. Weisberg (1993) A description of COADS surface meteorological fields and the implied Sverdrup transports for the Atlantic ocean from 20 Degrees to 60 Degrees N. *Journal of Physical Oceanography* **23** (10), 2201-2221

Méndes, M. and V. Magaña (2010) Regional Aspects of Prolonged Meteorological Droughts over Mexico and Central America. *American Meteorological Society* **23**, 1175-1188

Menzel D.W., and J.H. Ryther (1961) Annual variation in primary productivity of the Sargasso Sea off Bermuda. *Deep Sea Research* **7**, 282-288

Miller, J. et al., (2009) Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. *Coral Reefs* **28**(4), pp.925–937.

Müller-Karger, F.E., C.R. McClain, T.R. Fisher, W.E. Esaias, and R. Varela (1989) Pigment distribution in the Caribbean Sea: Observations from space. *Progress in Oceanography* **23**, 23-64

Mumby, P.J. et al. (2007) Thresholds and the resilience of Caribbean coral reefs. *Nature* **450**, 98–101

Muthiga, N.A. and A.M Szmant (1987) The effects of salinity stress on the rates of aerobic respiration and photosynthesis in the hermatypic coral *Siderastrea siderea* (1987) *Biological Bulletin* **173** (3), 539-551.

Newman, M., G.P. Compo, and M.A. Alexander (2003) ENSO-Forced Variability of the Pacific Decadal Oscillation. *Journal of Climate* **16** (23): 3853–3857

Nie, B., Chen, T., Liang, M., Wang, Y., Zhong, J., Zhu, Y., 1997. Relationship between coral growth rate and sea surface temperature in the northern part of South China Sea during the past 100 a. *Sci. China* **40**, 173–182.

Nyberg, J. B.A. Malmgren, A. Winter, M.R. Jury, H.K. Kilbourne and T.M. Quinn (2007) Low Atlantic hurricane activity in the 1970s and 1980s compared to the past 270 years. *Nature* **447**, 698-701

Ramsay, P., Cohen, A.L., 1997. Coral paleoclimatology research on the southeast African shelf. In: Lessios, H.A., Macintyre, I.G. (Eds.), *Proc. 8th Int. Coral Reef Symp., Smithsonian Research Institute,* Panama, 2, pp. 1731–1734.

Reaka-Kudla, M. L. (1997) The Global Biodiversity of Coral Reefs: A Comparison with Rain Forests. In Biodiversity II, M. L. Reaka-Kudla, D. E. Wilson, E. O. Wilson, Eds. (Joseph Henry Press, Washington, DC, 1997), pp. 83-108.

Roemmich, D. (1981) Circulation of the Caribbean Sea: A well-resolved inverse problem. *Journal of Geophysical Research* **86**, 7993-8005.

Roff, G. and P.J. Mumby (2012) Global disparity in the resilience of coral reefs. *Trends in Ecology and Evolution* **27**, 404-413.

Sarmiento, J.L., N. Gruber, and M.A. Brzezinski (2004) High-latitude controls on thermocline nutrients and low latitude biological productivity. *Nature* **427** (6969), 56-60.

Schneider, N., and B.D. Cornuelle (2005). The Forcing of the Pacific Decadal Oscillation. *Journal of Climate* **18** (8): 4355–4372.

Sebens. K. P., Helmuth, B., Carrington, E. and B. Agius (2003) Effects of water flow on growth and energetics of the scleractinian coral *Agaricia tenuifolia* in Belize. *Coral Reefs* **22.**

Szmant-Froelich, A. (1983) Functional aspects of nutrient cycling on coral reefs. The Ecology of Deep and Shallow Coral Reefs, Symposia Series for Undersea Research, 133-39. Rockville, MD: NOAA, National Undersea Research Program.

Saenger C., Cohen A.L., Oppo D.W., Halley R.B. and Carilli J.E. (2009) Surface-temperature trends and variability in the low-latitude North Atlantic since 1552. *Nature Geoscience* **2** (7), 492-495.

Scoffin, T.P., A.W. Tudhope, B.E. Brown, H. Chansang, R.F. Cheeney (1992) Patterns and possible environmental controls of skeletogensis of *Porites lutea*, South Thailand. *Coral Reefs* **11**, 1-11.

Seager, R., A. Tzanova and J. Nakamura (2009) Drought in the Southeastern United States: Causes, variability over the Last Millennium, and the potential for future hydroclimate Change. *American Meteorological Society*, 5021-5045

Shinn, E.A., Smith, G.W., Prospero, J., and M. Betzer (2000) African Dust and the Demise of Caribbean Coral Reefs. *Geophysical Research Letters* **27**, 3029-2032

Slowey, N.C., Crowley, T.J., (1995) Interdecadal variability of Northern Hemisphere circulation recorded by Gulf of Mexico corals. *Geophysical Research Letters* **22**, 2345–2348.

Smith, S.V. and R.W. Buddemeier (1992) Global Change and Coral Reef Ecosystems. *Annual Review of Ecology and Systematics* **23**, 89-118.

Smith S.V. and D.W. Kinsey (1976) Calcium-carbonate production coral reef growth and sea level change. *Science* **194** (4268), 937-939

Spence J.M., M.A. Taylor and A.A. Chen (2004) The effect of concurrent sea surface temperature anomalies in the tropical Pacific and Atlantic on Caribbean rainfall. *International Journal of Climatology* **24**, 1531–1541.

Stommel, H (1957) A survey of ocean current theory. *Deep Sea Research* **4** (3), 149-184.

Sutton, R. T and L. R. Hodson (2005). Atlantic forcing of North American and European summer climate. *Science* **309**, 115–118.

Tacio, H. (2008) Coral Reefs: Medicine Cabinets for the 21st Century. The Daily Guardian. September 25.

Talley, L.D, G.L. Pickard, J.E. William, and J.H. Swift (2011) Descriptive Physical Oceanography: An introduction. Elsevier, London, UK

Tanzil, J., Brown, B., Tudhope, A. & Dunne, R. (2009) Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between 1984 and 2005. *Coral Reefs* **28,** 519–528.

Taylor M.A., D.B. Enfield, and A.A. Chen (2002) The influence of the tropical Atlantic vs. the tropical Pacific on Caribbean Rainfall. *Journal of Geophysical Research* **107**(c9): 3127.

TEEB (2009) TEEB Climate Issues Update, September 2009

Thompson R. and T.J. Golding (1981) Tidally induced upwelling by the Great Barrier Reef. *Journal of Geophysical Research – Oceans and Atmospheres* **86**, 6517-6521.

Torres-Valdes, S., V.M. Roussenov, R. Sanders *et al.* (2009) Distribution of dissolved organic nutrients and their effect on export production over the Atlantic Ocean. *Global Biogeochemical Cycles* **23.**

Trenberth, K. and D.J. Shea (2005) Atlantic hurricanes and natural variability in 2005. *Geophysical Research Letters* **33.**

Trenberth, K.E., P.D. Jones, P. Ambenje, R. Bojariu , D. Easterling, A. Klein Tank, D. Parker, F. Rahimzadeh, J.A. Renwick, M. Rusticucci, B. Soden and P. Zhai. (2007) "Observations: Surface and Atmospheric Climate Change". In Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press. pp235–336.

Vasquez-Bedoya, L.F., Cohen, A.L., Oppo, D.W., and P. Blanchon (2012) Corals Record Persistent Multidecadal SST Variability in the Atlantic Warm Pool since 1775AD. *Paleoceanography*

Visbeck, M.H., J.W. Hurrell, L. Polvani et al. (2001) The North Atlantic Oscillation: Past, present, and future. *Proceedings of the National Academy of Sciences of the United States of America* **98** (23), 12876-12877.

Yap, H.T., and E.D. Gomez (1984) Growth of *Acroporal Pulchra*: II. Responses of natural and transplanted colonies to temperature and day length. *Marine Biology* **81**, 209-215

Wang, C. (2007) Variability of the Caribbean Low-Level Jet and its relations to climate. *Climate Dynamics* **29** (4), 411-422.

Williams, A., R.G. Roussenov and M.J. Follows (2006) Nutrient streams and their induction into the mixed layer. *Global Biogeochemical Cycles* **20** (1).

World Resources Institute (2004). Technical notes on methods and data sources available online at http://reefsatrisk.wri.org.

Zhang, R. and T. Delworth (2006) Impact of Atlantic multidecadal oscillations on India/Sahel rainfall and Atlantic hurricanes. *Geophysical Research Letters* **33**