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Short and Long-term Ramifications of Climate Change upon Coral Reef Ecosystems: Case Studies Across Two Oceans

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SHORT AND LONG-TERM RAMIFICATIONS OF CLIMATE CHANGE
UPON CORAL REEF ECOSYSTEMS: CASE STUDIES ACROSS TWO
OCEANS

By

Derek Paul Manzello

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

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World-wide coral reefs are in a state of decline as a result of many local and regional factors. Recent global mass mortalities of reef corals due to record warm sea temperatures have led researchers to consider global warming as one of the most significant threats to the persistence of coral reef ecosystems over the next 100 years. It is well established that elevated sea temperatures cause widespread coral bleaching, yet confusion lingers as to what facet of extreme temperatures is most important. Utilizing long-term *in situ* datasets, nine thermal stress indices were calculated and their effectiveness at segregating bleaching years *a posteriori* for multiple reefs on the Florida Reef Tract was tested. Simple bleaching thresholds based on deviations above the climatological maximum monthly sea temperature were just as effective at identifying bleaching years as complex thermal stress indices. Near real-time bleaching alerts issued by NOAA's Integrated Coral Observing Network (ICON) are now based upon a running 30-day average SST, such that alerts are only issued when the running 30-day average SST exceeds the estimated bleaching threshold for a particular site. In addition to three widespread, mass-coral bleaching events, the Florida Reef Tract was impacted by three tropical storms and 12 hurricanes from 1997-2005. Sea surface cooling associated with the high frequency of hurricanes that impacted Florida in 2005 likely acted to ameliorate the severity and duration of

bleaching. Nonetheless, hurricane-associated cooling is not expected to nullify the proposed effects of climate change on coral reefs. The role of thermal stress in coral bleaching has been extensively studied for eastern tropical Pacific (ETP) coral reefs. However, the ETP presents a unique opportunity as this region has sub-optimal conditions for coral reef development because of upwelling of CO_2-enriched water along the shallow thermocline. This upwelling results in a depressed aragonite saturation state (Ω_{arag}), which is likely an additional factor in the poor reef development throughout the ETP. The highest Ω_{arag} values documented in this study occur in the Gulf of Chiriquí, which corresponds with the greatest reef development of the entire ETP. Seasonal upwelling had a significant effect on the carbonate chemistry of surface waters in Pacific Panamá. This regionally-depressed Ω_{arag} of the ETP appears to result in corals with a less dense skeleton. Density values of poritid corals from the Galápagos, where Ω_{arag} was the lowest documented in this study, were significantly less dense relative to those from Panamá and the Great Barrier Reef. The density of non-living pocilloporid framework components were no different across the ETP carbonate saturation gradients. This could be a result of the activity of boring sponges removing the primary carbonate material within the dead coral skeleton, thus lowering density, albeit physical-chemical dissolution cannot be ruled out. These studies provide real-world examples of the ramifications of global climate change upon coral reef ecosystems.

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Chapter 1: Sea surface temperature (SST) variability on the Florida Reef Tract: relationship to coral bleaching events

Introduction

World-wide, coral reefs are in a state of decline as a result of many local and regional-scale factors. The persistence of coral reefs over the next century has been questioned due to the negative consequences of proposed climate change scenarios (Hoegh-Guldberg, 1999). Anthropogenic forced climate change models predict continued and accelerated global warming due to rising concentrations of the greenhouse gas, carbon dioxide (CO_2), primarily from the unregulated combustion of fossil fuels since the industrial revolution (IPCC, 2007). Global mean surface temperature has increased approximately 0.74^oC in the past 100 yrs and is expected to increase by no less than 1.5^oC further by they year 2100 (IPCC, 2007). Proposed increases in temperature are of concern because reef-building corals live at or near their upper thermal limits (Glynn, 1993). Temperature anomalies of 1^oC sustained for one month during the warmest part of the year have been shown to correlate with mass-coral bleaching events (Glynn, 1993; Goreau and Hayes, 1994; Brown, 1997; Hoegh-Guldberg, 1999). The Florida Reef Tract is no exception to this global trend and has been impacted by three separate widespread, mass-coral bleaching events from 1997-2005. Little work has been done on the phenomenon of coral bleaching in the Florida Keys; therefore, there is an urgent need to quantify and better understand the critical environmental limits expected to cause large-scale ecosystem disturbances (*i.e.*, coral bleaching) as a first step towards a better risk assessment of climate change impacts.

Coral bleaching (loss of symbiotic zooxanthellae and/or their pigments) is a stress response that can be caused by many adverse environmental conditions;

however, high sea temperature has been repeatedly identified as the most important causal factor at large spatial scales (Glynn, 1993; Brown, 1997; Hoegh-Guldberg, 1999; Berkelmans, 2002a). Coral bleaching events have been reported with increasing frequency on the Florida Reef Tract over the past 25 years. Isolated bleaching events occurred in 1911, 1961, 1973, and 1983 (Mayer, 1914; Shinn, 1966; Jaap, 1979, 1985), whereas the first event spanning the entire reef tract occurred in 1987 (Causey, 2001). Bleaching events in the 1980s were limited to the offshore reef tract, but in 1990 hydrocorals (*Millepora* spp.) on inshore patch reefs and the outer reef tract bleached (Causey, 2001). The most widespread and severe bleaching events have occurred during the past 10 years in 1997, 1998, and 2005, punctuated by mild and more localized bleaching events in the interim.

The variability in severity of bleaching both within and between sites is understandable given the complexity of the bleaching response. There is a broad continuum of pigment state (color) in zooxanthellate corals that is a function of temperature, light, and exposure time (Fitt *et al*., 2001), as corals naturally go through seasonal changes in zooxanthellae densities (Fitt *et al*., 2000). Although normal seasonal changes do occur in zooxanthellae densities, Warner *et al*. (2002) found that corals in the *Montastraea* species complex can lose up to 90% of their zooxanthellae without showing obvious signs of bleaching. Thus, visibly discernable paling in corals is a considerable metabolic stress to the coral host and should not be misinterpreted as normal just because zooxanthellae densities vary seasonally. Furthermore, inter- and intra-specific variability exists in the susceptibility of the coral host (Knowlton *et al*., 1992; Edmunds, 1994) and zooxanthellae (Rowan *et al*., 1997) to temperature stress.

Although the response of corals to elevated temperatures is highly complex, a number of indicators have been generated with temperature data to hind-cast and forecast bleaching episodes. Monthly mean sea temperatures above a local threshold (Goreau *et al*., 1993; Brown *et al*., 1996) as well as cumulative heat stress have been used to explain bleaching events (Gleeson and Strong, 1995; Podesta and Glynn, 1997). Berkelmans *et al*. (2004) found that 3-day maximum temperatures best correlated with spatial patterns of bleaching on the Great Barrier Reef, whereas a log-log linear relationship existed between temperature and number of days above that temperature at which bleaching occurred in Puerto Rico (Winter *et al*., 1998). Sammarco *et al*. (2006) re-evaluated the Puerto Rico dataset and showed warm, bleaching years were characterized by high variance in bi-weekly sea temperature whereas a lower variance in temperature occurred during warm, non-bleaching years.

To assess which aspects of temperature best explained bleaching years on the Florida Reef Tract, nine separate indices representing three facets of thermal stress were calculated: 1) short-term, acute temperature stress; 2) cumulative temperature stress; and 3) temperature variability. In addition, daily and monthly anomalies were calculated from derived seasonal cycles for Florida reef sites. Lastly, estimated bleaching thresholds for Florida were compared with those for the Bahamas and St. Croix, U.S. Virgin Islands.

Methods

SEAKEYS data

The SEAKEYS (Sustained Ecological Research Related to Management of the Florida Keys Seascape) program began in 1989 to complement the National Data Buoy Center's (NDBC) Coastal-Marine Automated Network (C-MAN) (Ogden *et al*., 1994). The SEAKEYS network was implemented for long-term monitoring of

meteorological and oceanographic conditions along the 220-mile Florida Reef Tract and Florida Bay encompassing the Florida Keys National Marine Sanctuary (FKNMS). For the purpose of this study only those SEAKEYS stations that are situated on the Florida Reef Tract were of interest. These are Fowey Rocks (25.59°N, 80.1°W, at the northern terminus of the Florida Reef Tract), Molasses Reef (25.01°N, 80.38°W, east of Key Largo), Sombrero Reef (24.63°N, 81.11°W, south of Marathon), Sand Key (24.46°N, 81.88°W, south of Key West), and the Dry Tortugas (24.64°N, 82.86°W, at the western end of the Florida Reef Tract) (Figure 1.1). From these stations hourly averages of bulk *in situ* sea surface temperature (SST) were obtained. Daily average SST was calculated from the beginning of data acquisition at each site through to 2005. The Molasses Reef site provided the most complete data set beginning in 1988 (Table 1.1). Data collection began at Sombrero Reef in 1988 as well, but data is limited at this site for some years. Data from the station at the Dry Tortugas is the least complete with large gaps during critical warm summer periods in 1997, 2004, and 2005. The remoteness of this station and the frequent impact of hurricanes in 2004 and 2005 explain why this site recorded only 82.7% of hourly data from 1992-2005 (Table 1.1). Nevertheless, all sites except the Dry Tortugas provide a record that is > 90% complete for hourly, *in situ* SST from the time of their installation through 2005.

Thermal stress indices and anomalies

The annual maximum daily average and hourly SSTs were calculated to assess if short-term extreme temperatures were related to bleaching. Maximum monthly mean SST and degree-days were used as indices of cumulative heat stress per year. Degree-days were calculated according to Podesta and Glynn (1997). This index is similar to the degree-heating weeks of Gleeson (1994) and Gleeson and Strong
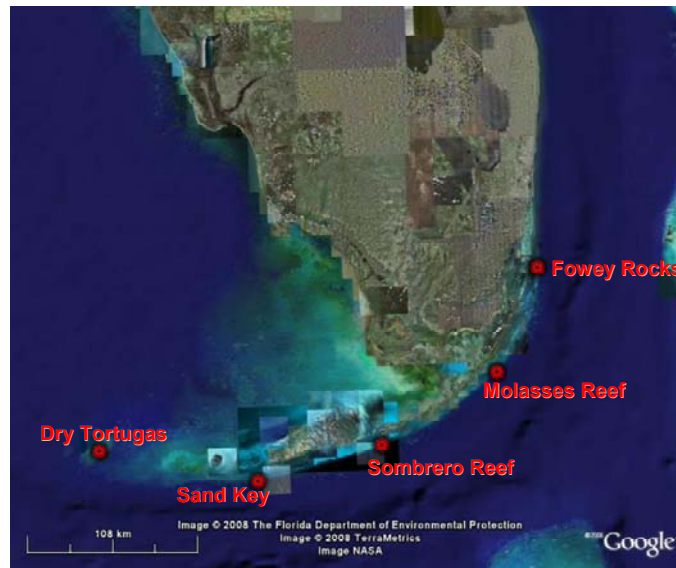
Figure 1.1. Satellite image showing the location of five SEAKEYS sites (labeled in red) situated on the Florida Reef Tract. (Image source: http://googleearth.com)

Table 1.1. Description and completeness of data by site from 1988-2005. N is number of days.

	Fowey Rocks	Molasses Reef	Sombrero Reef	Sand Key	Dry Tortugas
Start date	8/1/1991	1/1/1988	2/10/1988	5/19/1991	12/9/1992
N	5155	6460	5960	4994	4224
% complete	94.2	98.3	90.7	91.2	82.7

(1995). The number of days per year that daily SSTs were $> 29.5^{o}$C, 30°C, 30.5^{o}C, and 31°C were calculated to assess their value as simple bleaching indices. These annual temperature variables were then logistically regressed with the presence-absence of bleaching. Only those years without missing data were used in the logistic regressions totaling 58 non-bleaching years and 12 bleaching years for Florida sites. The role of temperature variability was assessed by computing the coefficient of variation (CV) in bi-weekly mean SST from 1 July to 31 October and then comparing the CVs of warm, non-bleaching (WNB) and warm, bleaching (WB) years by site (Sammarco *et al*., 2006). WNB and WB compared by site were: Fowey Rocks, WNB

(1993, 1999, 2004), WB (1997, 1998, 2005); Molasses Reef, WNB (1993, 1995, 2002), WB (1997, 1998, 2005); Sombrero Reef, WNB (2000, 2001, 2002), WB (1997, 1998, 2005); Sand Key, WNB (1995, 2001, 2004), WB (1993, 1997, 1998, 2005); Dry Tortugas, WNB (1999, 2000), WB (1997, 1998).

The seasonal SST cycle for each locale was estimated by taking the average of each day for the years of data available excluding warm years (1997, 1998, 2005 for all sites and 1993 for Sand Key only). This was done to eliminate any bias possibility introduced by anomalously warm years (e.g., ENSO years of 1997/98) in this relatively short record. For leap years, SST data for February 29 was not included in the estimate of the seasonal cycle. After determining the annual seasonal cycle for each site, the residuals (anomalies) from these values per year were determined daily and monthly. The time-series of monthly temperature anomalies were plotted during the warmest part of the year (July – September) for all sites, as these data were most pertinent to this study.

Time-integrated bleaching threshold curves

To determine thresholds for each site, beyond which community-wide bleaching is expected to commence, the cumulative number of days at each temperature ($0.1°C$ increments) were calculated each summer. These time-temperature curves represent the tail end of the cumulative frequency distributions of temperature for each year (Berkelmans, 2002a). A polynomial bleaching threshold curve was then interpolated through the average number of days at each $0.1°C$ increment of the warmest, non-bleaching year and the coolest bleaching year for each site. Cumulative temperature curves that lie above the threshold line indicate bleaching years, whereas those that fall below the threshold line indicate non-bleaching years (Berkelmans, 2002a). This is a simplification of the methods

previously described (Berkelmans, 2002a, 2002b), because the bleaching data used here were highly qualitative as a result of the paucity of comprehensive studies documenting bleaching on the Florida Reef Tract. For Sand Key, the threshold curve was modified at the right tail so that it was above the non-bleaching year of 2004. This technique is hypothesized to be more robust than thresholds estimated as accumulated heat stress (i.e., degree-days threshold value) as time-integrated thresholds do not falsely assume linearity in exposure time and temperature (Berkelmans, 2002a). Furthermore, threshold curves allow daily estimates of thermal stress accumulation in near real-time.

Bleaching threshold curves were determined for Salt River Bay, St. Croix, U.S. Virgin Islands (17.784°N, 64.761°W) and North Norman's Patch Reef, Lee Stocking Island, Bahamas (23.791°N, 76.139°W). SST was measured *in situ* with a Falmouth Scientific CTD affixed at 1 m depth (nominal) to the National Oceanic and Atmospheric Administration (NOAA) Integrated Coral Observing Network (ICON) stations in St. Croix (operational since 2002) and the Bahamas (operational since 2003). Due to the temporal constraints associated with the ICON data, seasonal cycles, anomalies, and thermal stress indices (excluding threshold estimates) were not calculated. Seasonal maximum SST was determined from advanced very high resolution radiometer (AVHRR) satellite data for all SEAKEYS and ICON sites. Satellite SST data was only used to estimate the seasonal maximum at all sites; all other SST values reported were measured *in situ*. Satellite data were used to determine the seasonal maximum given that the ICON datasets were not long enough to reliably estimate seasonal cycles. The cumulative frequency distribution of temperature from 2003 was used as the bleaching threshold curve for St. Croix as a partial bleaching event was documented during this year at this site (Manzello *et al.*,

2006). The bleaching threshold for the Bahamas was estimated by averaging the number of days at each $0.1^{\circ}C$ increment for 2005 (bleaching year) and 2006 (warmest, non-bleaching year). Bleaching thresholds were also determined by taking the mean of the minimum monthly SST associated with bleaching and the maximum monthly SST not associated with bleaching for all SEAKEYS and ICON sites. Minimum monthly SST associated with bleaching refers to the coolest annual maximum monthly SST associated with a bleaching year, whereas the maximum monthly SST not associated with bleaching refers to the warmest annual maximum monthly SST not associated with a bleaching year.

Bleaching and coral community structure

Information on coral bleaching events for the Florida Reef Tract were obtained from an exhaustive search of the literature, available bleaching reports archived on the internet (Reefbase, 2006; CHAMP, 2006), and correspondence with local researchers. Given the spatial variability in environmental conditions and bleaching, a 15 km radius was chosen around each station and all bleaching reports made for reefs or coral communities within these bounds were compiled. Each bleaching observation was categorized based on severity (Table 1.2). A 'bleaching year' was identified when more than one bleaching report detailed moderate or mass bleaching (score of 2 or 3, respectively, in Table 1.2) or a local researcher corroborated an event. Mild bleaching (*i.e.*, only a subset of coral species show paling and only a small proportion of all colonies (< 25%) bleach; score of 1 in Table 1.2) observations were ignored because these reports may represent confusion with the normal seasonal patterns in zooxanthellae densities for some coral species (Fitt *et al*., 2000). Moderate bleaching is defined as > 25%, but < 50% of all coral colonies paling. Mass bleaching is when > 50% of all coral colonies are bleached. NOAA ICON personnel on SCUBA have

documented bleaching in St. Croix since 2003. Mass bleaching occurred in 2005, whereas a mild, partial bleaching event occurred in 2003 (Manzello *et al.*, 2006). Mass coral bleaching was documented at North Norman's Patch Reef in 2005 (Mueller, unpub. data).

Table 1.2. Bleaching events and severity within 15 km radius of SEAKEYS sites (1992-2005).

Year	Site	Bleaching category
1993	Sand Key	2
1997	Fowey Rocks	3
1997	Molasses Reef	3
1997	Sombrero Reef	3
1997	Sand Key	3
1997	Dry Tortugas	3
1998	Fowey Rocks	3
1998	Molasses Reef	3
1998	Sombrero Reef	3
1998	Sand Key	3
1998	Dry Tortugas	3
2001	Sombrero Reef	1
2004	Sombrero Reef	1
2005	Fowey Rocks	3
2005	Molasses Reef	2
2005	Sombrero Reef	3
2005	Sand Key	2

Mild bleaching (score of 1) is when only a subset of coral species show paling and only a small proportion of all colonies (< 25%) bleach. These observations were ignored for delineation of thresholds because these reports may represent confusion with the normal seasonal patterns in zooxanthellae densities for some coral species (Fitt *et al.*, 2000). Moderate bleaching (score of 2) is defined as > 25%, but < 50% of all coral colonies paling. Mass bleaching (score of 3) is when > 50% of all coral colonies are bleached.

The structure of coral communities is an important determinant to the susceptibility and severity of bleaching at a site (Marshall and Baird, 2000; McClanahan *et al.*, 2007). Hermatypic coral species abundance data were collected in 2003 and 2006 for Florida reef sites within 15 km of the SEAKEYS sites (Marks and Lang, 2006); 1999 for reefs near (< 15 km) Salt River Bay, St. Croix (Marks and Lang, 2006); and 2005 before and during bleaching at North Norman's Patch Reef in the Bahamas (Mueller, unpub. data). Although these data are not directly comparable because they were collected in different years, they nonetheless provide an idea of the species composition at the sites for which bleaching thresholds were derived.

Community bleaching susceptibility Index

The five most common coral species at all sites were given a score based on their reported susceptibility to bleaching: 1 = high susceptibility; and 2 = low susceptibility. *Millepora* spp., *Agaricia* spp., *Siderastrea siderea*, and *Montastraea annularis* (spp. complex) were assigned a score of 1, whereas all other coral species were assigned a score of 2 (Jaap, 1979, 1985; CARICOMP, 1997; McField, 1999). The five most abundant coral species by site were ranked so that the species with the highest abundance received a score of 5; the second most abundant species received a score of 4 and so on. For each site, the abundance ranks (1-5) of each species were multiplied by their respective susceptibility scores, and the resulting products were summed to produce a scaled estimate of reef-wide bleaching susceptibility. A low site susceptibility score (min. = 15) indicates a site with a community structure highly susceptible to bleaching whereas a high score (max. = 30) indicates a site resistant to bleaching.

Results

Florida Reef Tract: Seasonal cycles and sea temperature anomalies

Anomalously warm temperatures coincided with every bleaching event examined (Fig. 1.2). Monthly anomalies coincident with bleaching in 2005 were not excessively high and were positive only during August for most sites. Bleaching in 2005 was associated with an August anomaly of $0.6^{o}C$ at Molasses Reef, $0.7^{o}C$ at Fowey Rocks and Sand Key, and $0.8^{o}C$ at Sombrero Reef. Bleaching occurred at Sand Key in August 1993 with an anomaly of only $0.5^{o}C$, yet bleaching was not reported at Fowey Rocks or Sombrero Reef with the same anomaly in August 1993 or 2003, respectively (Fig. 1.2).
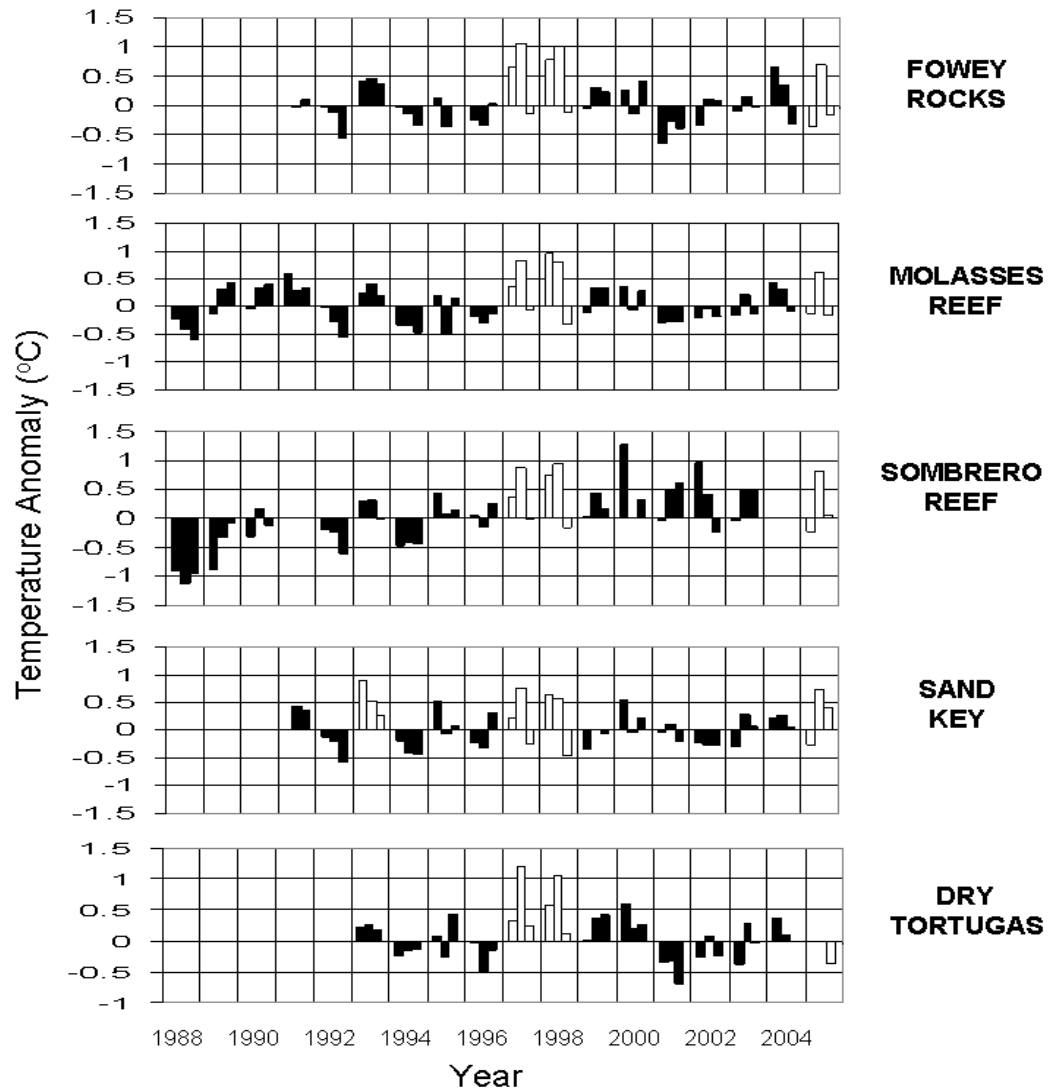
Figure 1.2. Time series of monthly mean temperature anomalies at Florida sites from July to September, 1988-2005. Each bar represents one month. Open bars identify bleaching years.

The timing of the warm and cool peaks of the seasonal cycles was similar for all sites examined, with the coolest and warmest part of the year in January and August, respectively (Table 1.3). Molasses Reef had the smallest annual range in sea temperature, whereas the Dry Tortugas had the greatest (Table 1.3). Sombrero Reef

was the warmest of these sites with the greatest maximum daily average sea temperature and overall mean sea temperature.

Table 1.3. Minimum, mean, maximum, and amplitude of the seasonal cycle for SEAKEYS stations on the Florida Reef Tract. Values in degrees Celsius.

	Fowey Rocks	Molasses Reef	Sombrero Reef	Sand Key	Dry Tortugas
Minimum	22.6	23.2	22.7	22.1	21.5
Date(s) of min.	Jan. 25	Jan. 28	Jan. 25-26	Jan. 25	Jan. 27-29
Mean	26.5	26.7	26.8	26.5	26.1
Maximum	30.2	30.1	30.6	30.3	30.3
Date(s) of max.	Aug. 20-21	Aug. 10-23	Aug. 10-12	Aug. 15	Aug. 25
Amplitude	7.6	6.9	7.9	8.2	8.8

Florida Reef Tract: Bleaching indices and thresholds

Maximum monthly SST and the number of days $> 30.5^{\circ}$C were the best indices of those examined (Table 1.4). The maximum monthly SST coincident with bleaching was variable by site; however it was always $\geq 30.5^{\circ}$C. Degree-days alone were very poor indicators of bleaching years (Table 1.4; Fig. 1.3). Degree-day values were plotted against maximum monthly sea temperature as this representation was a good indicator of bleaching years for eastern Pacific coral reefs (Podesta and Glynn 1997). These plots worked well by segregating bleaching from non-bleaching years; however, as a measure of thermal stress, the degree-day values themselves were very poor predictors of bleaching (Fig. 1.3). Fowey Rocks had 22 days of missing data in the three summer months of 2005, which explains why this point is not clumped closer to 1997 and 1998 (Fig. 1.3). In spite of these missing data, it is still clear that Fowey Rocks was exceptionally warm in 2005. Although useful in segregating bleaching from non-bleaching years, these plots were not helpful for determining actual bleaching thresholds (*i.e.*, the upper limit in cumulative temperature stress where bleaching is expected). Delineating the location of an estimated bleaching threshold using these plots would be qualitative and arbitrary.
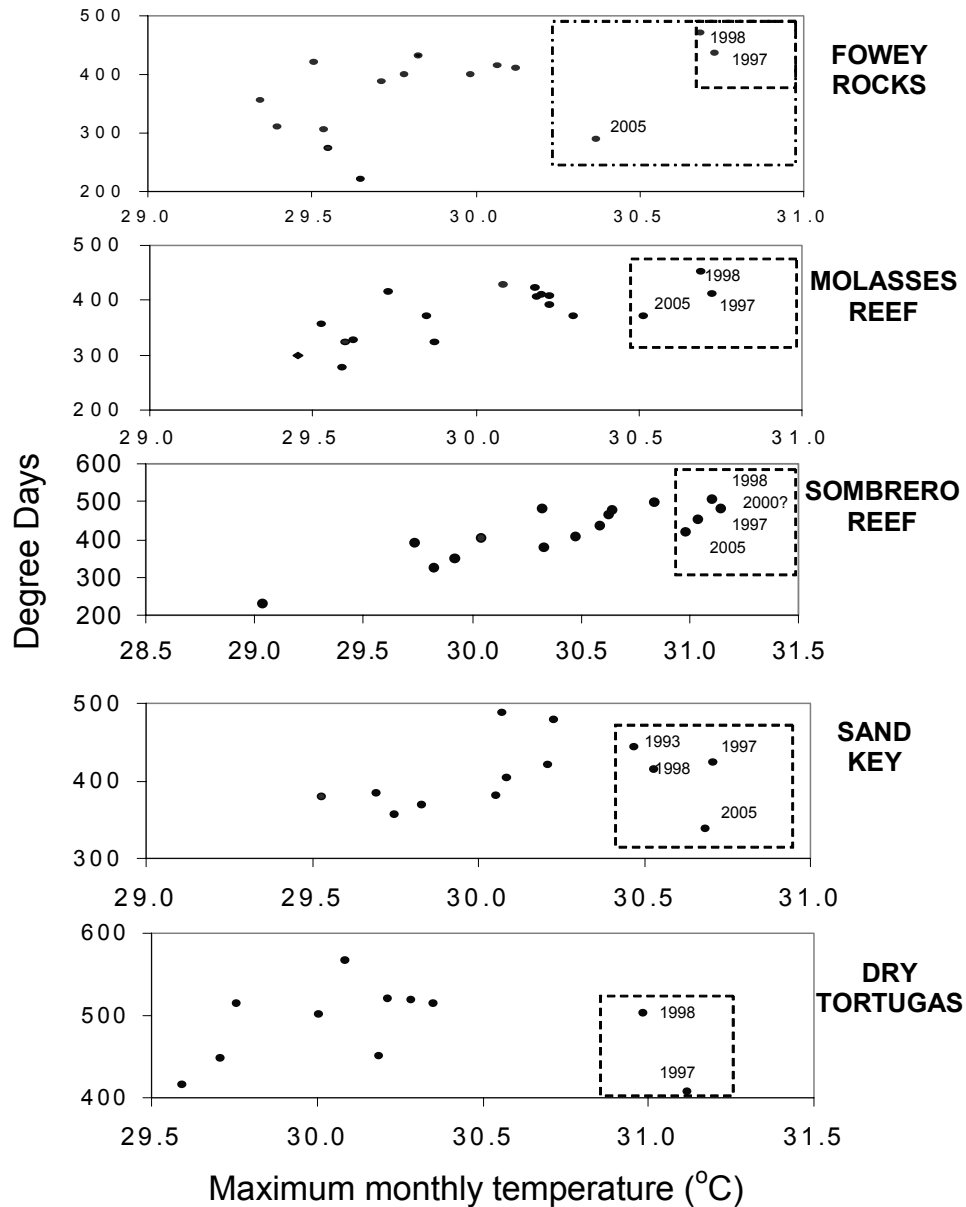
Figure 1.3. Degree days versus annual maximum monthly mean sea temperature at all sites. Major bleaching years enclosed in dashed boxes. Note that temperature scales of graphs differs.

The bleaching threshold curves are situated very near the warmest non-bleaching years for all sites (Fig. 1.4). The warmest non-bleaching years varied by site highlighting the patchiness of temperature disturbances. A threshold curve could not be determined with confidence for Sombrero Reef as the warm, non-bleaching summer of 2000 exceeded the time-temperature curves of bleaching years. The CVs

of bi-weekly SST for warm bleaching years were not significantly different from warm, non-bleaching years (Mann-Whitney U-tests, p-values ranged from 0.47 – 0.98). Monthly SST bleaching thresholds were similar for Florida sites, although the threshold for Sombrero Reef was warmer than the other sites by 0.4-0.5°C (30.4°C for Fowey Rocks, Molasses Reef, and Sand Key; 30.5°C for the Dry Tortugas; 30.9°C for Sombrero Reef).

Table 1.4. Relevant statistics for logistic regression of bleaching indices with presence-absence of bleaching.

Index	r^2	χ^2	p
Days > 29.5 °C	0.13	8.6	0.0033
Days > 30°C	0.32	20.3	< 0.0001
Days > 30.5°C	0.42	27.1	< 0.0001
Days > 31°C	0.22	14.2	0.0002
Hourly Max. SST	0.12	7.5	0.0063
Daily Max. SST	0.2	12.8	0.0003
Monthly Max. SST	0.55	35.1	< 0.0001
Degree-days	0.06	3.7	0.055

Comparison of bleaching thresholds for Florida, Bahamas, and St. Croix

Bleaching threshold curves constructed for the Bahamas and St. Croix, U.S. Virgin Islands are shown alongside those for Florida in Fig. 1.5. Estimates of bleaching thresholds based on monthly SSTs and the intercept of the bleaching curves were correlated (r^2 = 0.93, p = 0.0017). The monthly SST bleaching thresholds were cooler for the Bahamas (29.8°C) and St. Croix (29.4°C) compared to Florida (Table 1.5). There is a suggestion of an inverse latitudinal trend in the estimated monthly SST bleaching thresholds (r^2 = 0.68, p = 0.02), but a better relationship exists between bleaching thresholds and seasonal maximum SST (r^2 = 0.80, p = 0.007) (Fig. 2.6). The same trends were apparent when bleaching thresholds based on the intercept of the bleaching curves were regressed with latitude (r^2 = 0.77, p = 0.0217) and seasonal maximum SST (r^2 = 0.90, p = 0.0038).

Coral species abundance and bleaching susceptibility by site is listed in Table 1.6. The site with the community structure most resistant to bleaching was St. Croix
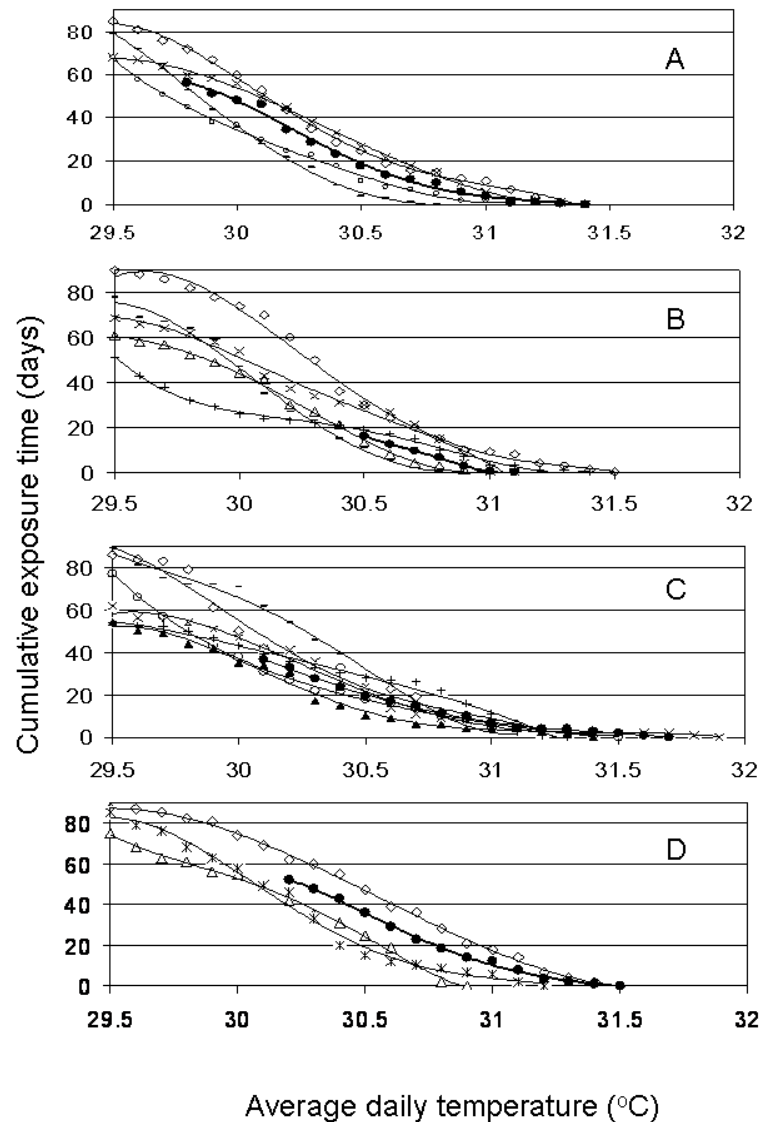
Figure 1.4. Bleaching threshold curves for Florida reef sites: (A) Fowey Rocks, (B) Molasses Reef, (C) Sand Key, and (D) the Dry Tortugas. Bleaching curves fitted with polynomial trend lines. (-) 1993; (x) 1997; (◊) 1998; (Δ) 1999; (ж) 2000; (▲) 2001; (○) 2004; (+) 2005. (●) Estimated bleaching curve. Cool, non-bleaching years were removed for clarity.

and Sand Key, Florida whereas the site most susceptible was North Norman's Patch Reef, Bahamas (Table 1.6). Community bleaching susceptibility was not related to the bleaching thresholds estimated as maximum monthly SST ($r^2 = 0.03$, $p = 0.73$), nor the intercepts of the bleaching curves ($r^2 = 0.06$, $p = 0.64$).
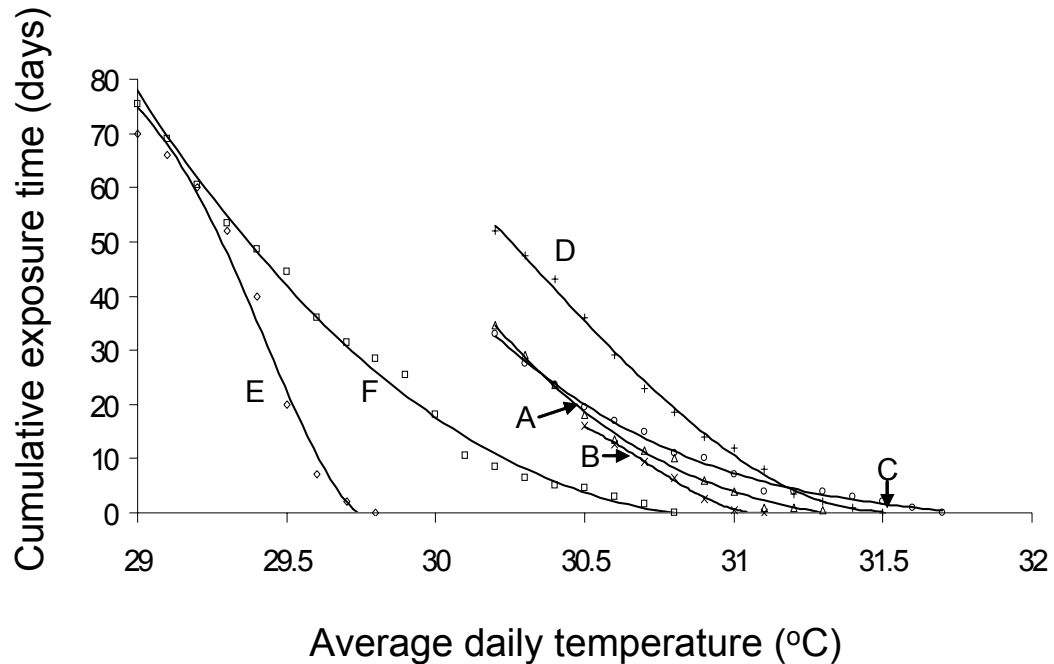
Figure 1.5. Comparison of bleaching threshold curves for: (A) Fowey Rocks, FL (B) Molasses Reef, FL (C) Sand Key, FL, (D) Dry Tortugas, FL, (E) St. Croix, (F) Bahamas.

Table 1.5. Bleaching thresholds estimated as a monthly SST*.

Site	Threshold (^{o}C)
Fowey Rocks, FL	30.4
Molasses Reef, FL	30.4
Sombrero Reef, FL	30.9
Sand Key, FL	30.4
Dry Tortugas, FL	30.5
Lee Stocking Island, Bahamas	29.8
St. Croix, US Virgin Islands	29.4

*Threshold determined by taking the mean of the minimum monthly SST associated with bleaching and the maximum monthly SST not associated with bleaching. Minimum monthly SST associated with bleaching refers to the coolest annual maximum monthly SST associated with a bleaching year, whereas the maximum monthly SST not associated with bleaching refers to the warmest annual maximum monthly SST not associated with a bleaching year.

Discussion

Anomalously warm temperatures in excess of the bleaching thresholds estimated herein were associated with every bleaching year. Maximum monthly sea surface temperature (SST) and the number of days > 30.5^{o}C were the most significant; indicating that cumulative exposure to temperature extremes characterized bleaching years (Goreau *et al*., 1993; Brown *et al*., 1996; Berkelmans, 2002a). The CVs of the

bi-weekly SSTs of warm, bleaching years were no different than those of warm, non-bleaching years showing that bi-weekly SST variability during summer months did not characterize bleaching years at any Florida sites, as shown for Puerto Rico (Winter *et al*., 1998; Sammarco *et al*., 2006). These data re-confirm that the thermal shock of fluctuating temperatures does not cause or correlate with widespread bleaching, but rather the prevailing mean temperatures are most critical (*e.g.*, Jokiel and Coles, 1990; Craig *et al*., 2001). Bleaching thresholds were not related to community susceptibility using the index herein, but were significantly related to seasonal maximum SST (Coles *et al*., 1976).

The bleaching curve technique was good for estimating thresholds as shown by the significant correlation between the intercepts of the bleaching curves and thresholds estimated as monthly SST. This technique was not applicable at Sombrero Reef due the overlap observed between bleaching and non-bleaching year curves. Thermal conditions appeared favorable for bleaching at Sombrero Reef in 2000, as maximum monthly SST (31.1^{o}C) was greater than the threshold (30.9^{o}C), yet bleaching was not reported. The apparent absence of bleaching was not explained by low variance in bi-weekly SST relative to bleaching years. It is important to note that this was the only false positive (*i.e.*, temperatures in excess of threshold without bleaching) for all sites totaling 77 years of data analyzed. The possibility of a community shift to more bleaching tolerant taxa following the temperature disturbances of 1997 and 1998 at Sombrero Reef was considered as a potential reason why bleaching was not reported in 2000 (McClanahan *et al*., 2007). Whether or not a community shift occurred is unknown, but maximum monthly SST for 2005 was the same as previous bleaching years (all 31.0^{o}C) implying that the bleaching threshold of the taxa at Sombrero Reef did not change with time or repeated bleaching.

Table 1.6. Relative abundance and bleaching susceptibility score of coral communities within 15 km of stations. LSI: Lee Stocking Island, Bahamas; FR: Fowey Rocks, Florida; MR: Molasses Reef, Florida; SR: Sombrero Reef, Florida; SK: Sand Key, Florida; DT: Dry Tortugas, Florida; STX: St. Croix, U.S. Virgin Islands. Year that surveys were performed is in parentheses following site abbreviation.

		LSI (2005)	FR (2003)	MR (2006)	SR (2003)	SK (2003)	DT (2004)	STX (1999)
No. sites surveyed		2	1	2	2	3	16	3
Mean Depth (± s.e.m.)		6 (0)	5.2 (0)	6.7 (1.27)	6.7 (1.31)	4.5 (0.76)	7.9 (0.27)	11.1 (0.66)
Total no. of corals		616	34	79	118	209	845	288
Coral Species	Suscept. Index*	% of total						
A. cervicornis	2	0.3	-	-	-	4.3	3.2	0.3
A. palmata	2	-	-	1.3	8.5	18.2	-	-
C. natans	2	-	2.9	-	6.8	1.9	7.7	3.1
Agaricia spp.	1	20.6	8.8	12.7	2.5	1.0	0.4	3.8
M. annularis spp. complex	1	3.9	5.9	13.9	6.8	7.7	30.2	28.5
S. siderea	1	6.5	26.5	2.5	21.2	7.2	9.2	12.5
P. astreoides	2	12.0	8.8	22.8	11.9	44.0	6.4	3.1
D. strigosa	2	2.9	-	1.3	3.4	0.5	3.2	3.1
D. labyrinthiformis	2	0.5	2.9	5.1	2.5	1.0	1.2	1.4
D. clivosa	2	-	2.9	-	4.2	0.5	0.7	-
M. cavernosa	2	1.9	2.9	6.3	12.7	5.7	21.3	42.7
M. meandrites	2	1.6	-	-	-	-	-	-
Millepora spp.	1	48.9	8.8	30.4	9.3	5.3	10.5	-
S. intersepta	2	0.8	2.9	1.3	4.2	2.4	3.3	-
P. porites	1	0.0	26.5	2.5	5.9	0.5	2.7	1.4
Site susceptibility score		18	22	20	22	25	19	25

*1 = high susceptibility to bleaching. 2 = lower susceptibility to bleaching
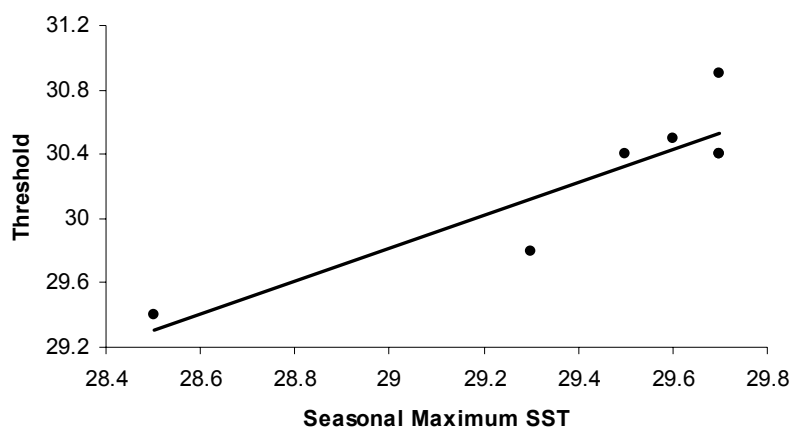
Figure 1.6. Seasonal maximum SST plotted against bleaching thresholds for Florida, Bahamas, and St. Croix ($r^2 = 0.80$, $p = 0.007$).

It is hypothesized that the local-scale oceanographic conditions and their influence on the subsurface light field experienced by coral colonies may partially explain the false positive at Sombrero Reef in 2000. Sombrero Reef is located adjacent to the wide channels between islands in the middle Florida Keys where there is a strong net outflow of turbid and sometimes "green" Florida Bay waters to the reef tract (Smith, 1994; Porter et al., 1999; Lee and Smith, 2002). Jokiel and Brown (2004) reported that corals in areas of high turbidity in Hawaii suffered little or no bleaching even though they experienced identical temperatures to bleached corals in clear waters and suggested that reduced light penetration likely explained these observations. A thermal bleaching threshold was exceeded without bleaching for a coral community inhabiting turbid intertidal waters in Phuket, Thailand (Dunne and Brown, 2001). The recent history of photosynthetically active radiation (PAR, 400-700 nm) experienced at the coral surface prior (~1 month) to thermal stress shaped the bleaching response (Brown et al., 2000, 2002). These studies highlight the ongoing need for a comprehensive understanding of the underwater light field (unavailable for this study) experienced by corals prior to and during thermal stress (see Dunne and Brown, 2001; Fitt et al., 2001; Brown et al., 2002).

A temperature anomaly of ~1oC above the mean monthly summer maximum is a frequently used threshold thought to explain severe bleaching (Goreau and Hayes, 1994; Gleeson and Strong, 1995; Hoegh-Guldberg, 1999). A monthly anomaly of $\geq$ 0.6oC above the seasonal maximum was coincident with moderate to severe bleaching on Florida reefs in 2005, which agrees with findings from Thailand (Brown et al., 1996). Hence, the commonly used ~1oC anomaly may be too conservative to identify all bleaching events.

Conclusions

The bleaching thresholds presented in this study will refine expert systems that generate automated warnings in near real-time when conditions are conducive to bleaching (Hendee *et al*., 2001). These systems augment the large-scale NOAA satellite based 'hotspot' early warning system (Strong *et al*., 1997), which lacks fine temporal and spatial resolution (McClanahan *et al*., 2007). Additionally, sea temperature data obtained through *in situ* monitoring stations are more accurate at local scales than that obtained via satellites (Berkelmans, 2002a). Continued environmental monitoring, specifically of the underwater light field (PAR and UV, see Dunne and Brown, 2001) in concert with field studies (see McClanahan *et al*., 2007) is required to test the future validity of the thresholds presented here. Hind-casts showed that monthly mean SST in excess of the local threshold explained all bleaching years, thus future refinements are expected to be minimal.

Chapter 2: SST response to hurricane passage on the Florida Reef Tract

Coral bleaching and hurricanes

In addition to three widespread, mass-coral bleaching events, the Florida Reef Tract was impacted by three tropical storms and 12 hurricanes from 1997-2005. Hurricane development is dependent on warm (> 26°C) sea temperatures (Gray, 1979) and often correlated with widespread bleaching events. A common physical effect of hurricane passage is a reduction in sea temperature (up to 5°C) caused by wind-forced vertical mixing (Cornillion *et al*., 1987; Price *et al*., 1994; Xie *et al*., 1998). It is well documented that physical impacts from storms can be devastating to coral reef ecosystems (Harmelin-Vivien, 1994), but the damage caused by storms is highly variable between and within affected reefs (Lirman and Fong, 1997). Severe damage to coral reefs has been observed and predicted to occur on reefs up to 30 to 90 km from a storm's center (Done, 1992; Woodley, 1992; Scoffin, 1993). Based on the spatial and temporal correlation between coral bleaching events and hurricanes, it has been hypothesized that bleached corals may benefit from hurricane passage due to the resultant sea surface cooling (Glynn, 1996). To better understand this potential feedback, the magnitude and duration of sea temperature cooling coincident with the passage of hurricanes and tropical storms was assessed for five reefs sites on the Florida Reef Tract from 1998-2005.

Methods

Environmental Data Analysis

Hourly averages of *in situ* sea temperature and wind speed were obtained from the same five aforementioned SEAKEYS stations. Daily average sea temperature and daily average wind speed were determined from 1998-2005 for these sites. The

difference between pre- and post-storm daily average sea temperature ($\Delta^{o}C$), the duration of cooling (number of days that sea temperature remained below the seasonal average), and the daily maximum wind speed due to storms was determined. The seasonal sea temperature cycle was estimated by taking the average of each day for the years of data available at each site and was smoothed by interpolating a sixth order polynomial using least squares. Data acquisition began in 1988 at Molasses and Sombrero Reef, 1991 at Fowey Rocks and Sand Key, and 1992 at the Dry Tortugas.

Regression analysis was used to evaluate the relationship between both $\Delta^{o}C$ and the duration of cooling with distance from the storm center and wind speed. Distance from the storm center was estimated as the nearest distance that the plotted coordinates of a storm track passed to a site (Unisys, 2006). The relationship between cooling patterns and the location of a site with respect to the track of the storm was tested with Analysis of Covariance (ANCOVA, tests for equal and unequal slopes). An alpha level of 0.05 was used for significance in all tests.

Results

Decreases in sea temperatures associated with high winds coincided with all hurricanes and tropical storms that passed within 700 km of the Florida Reef Tract (Table 2.1; Figures 2.1 – 2.4). Sea temperatures were cooled by 0.3 to 3.2^{o}C (mean ± s.e.m. = 1.5 ^{o}C ± 0.10, n = 53) by hurricanes or tropical storms whose tracks passed within 400 km of a site. When storms were > 400 km from a site, $\Delta^{o}C$ (magnitude of cooling) ranged from 0.1 to 0.9 ^{o}C (mean ± s.e.m. = 0.5 ^{o}C ± 0.09, n = 10). $\Delta^{o}C$ was significantly related to the nearest distance a storm track passed from a site and was greater when a site was to the left of the storm track (Table 2.2). Wind speeds at the sites were significantly correlated with their distance from the storm track, and

therefore related to Δ^oC (Table 2.2). For the same wind speed, Δ^oC was greater for

sites to the left of the storm track than the right (Table 2.2).

Table 2.1.   Nearest distance from and magnitude of cooling (Δ^oC: max., min.) associated with named storms that affected the Florida Reef Tract from 1998-2005.

Year	Storm name	Cat	Distance Value (Site)	Max. Δ^oC Value (Site)	Min. Δ^oC Value (Site)
1998	H Georges	2	46 (DT)	1.4 (MR, SK)	1.2 (FR, DT)
1999	H Floyd	4	300 (FR)	0.9 (MR, SR)	0.4 (DT)
1999	TS Harvey	TS	146 (FR)	1.3 (SR, SK)	0.7 (DT)
1999	H Irene	1	11 (SK)	1.3 (SR)	0.8 (MR)
2001	TS Gabrielle	TS	148 (DT)	3.2 (FR)	1.5 (MR, DT)
2001	H Michelle	1	222 (SR)	2.8 (SR)	1.6 (FR, SK)
2004	H Charley	2	29 (DT)	0.6 (SK)	0.3 (FR)
2004	H Frances	2	168 (FR)	2.2 (FR)	1.7 (MR)
2004	H Ivan	4	368 (DT)	0.5 (SK)	0.1 (FR)
2004	H Jeanne	3	181 (FR)	2.1 (FR)	1.0 (SK)
2005	TS Arlene	TS	226 (DT)	1.2 (SK)	0.4 (MR)
2005	H Dennis	1	66 (DT)	2.1 (SR)	0.7 (FR)
2005	H Katrina	1	39 (FR)	2.7 (DT)	1.3 (MR)
2005	H Rita	2	62 (DT)	1.4 (SR)	0.8 (MR)
2005	H Wilma	3	46 (DT)	3.0 (FR)	2.4 (MR, SR)

Abbreviations: Cat, Category of storm [Saffir-Simpson scale (Simpson and Riehl, 1981)] when it was noted distance from site; H, hurricane; TS, tropical storm; FR, Fowey Rocks; MR, Molasses Reef; SR, Sombrero Reef; SK, Sand Key; DT, Dry Tortugas.
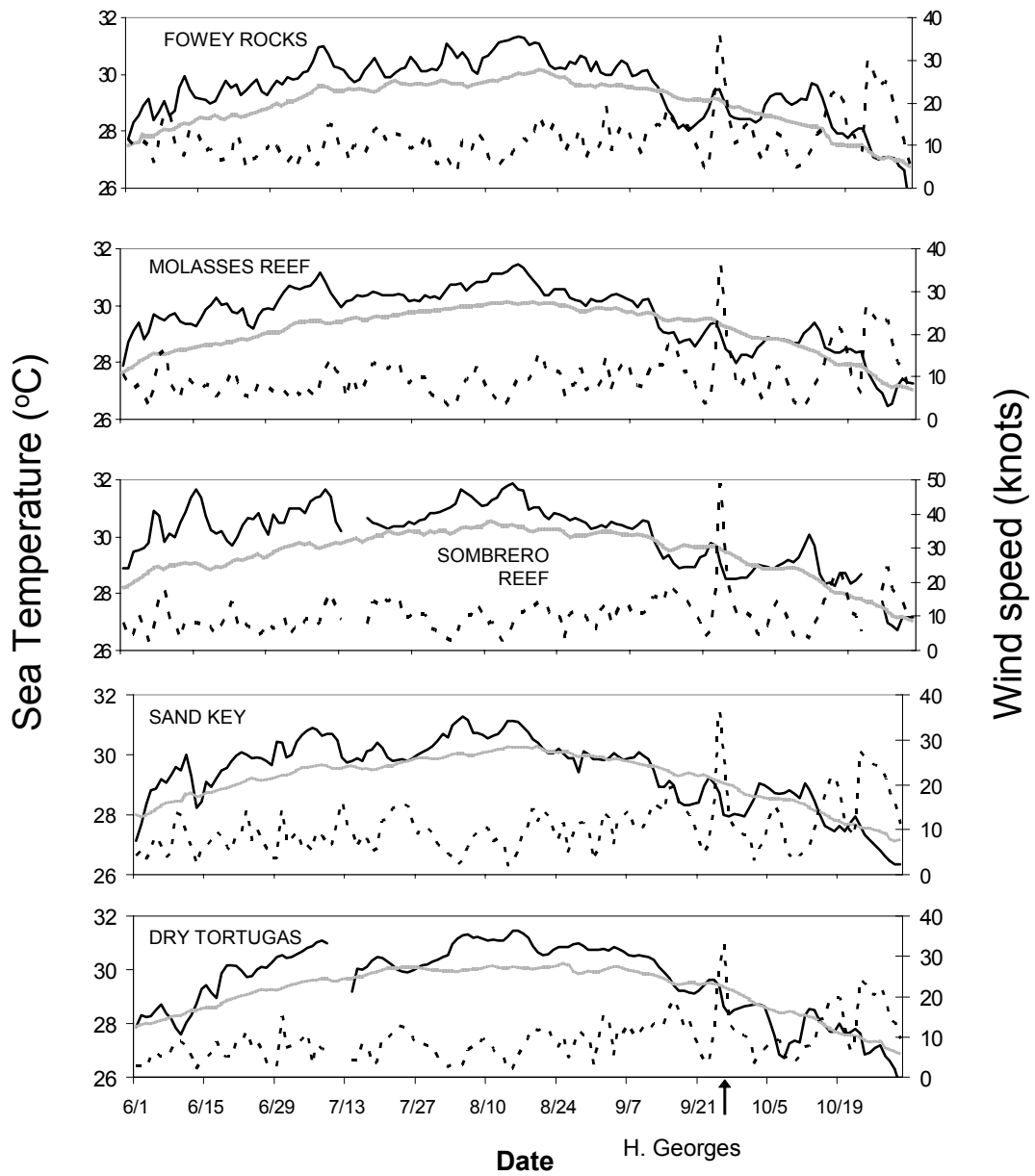
Figure 2.1. Daily average sea temperature (solid line) and wind speed (dashed line) for sites located along the Florida Reef Tract from 1 June – 31 October 1998. Shaded line is the seasonal cycle for sea temperature.
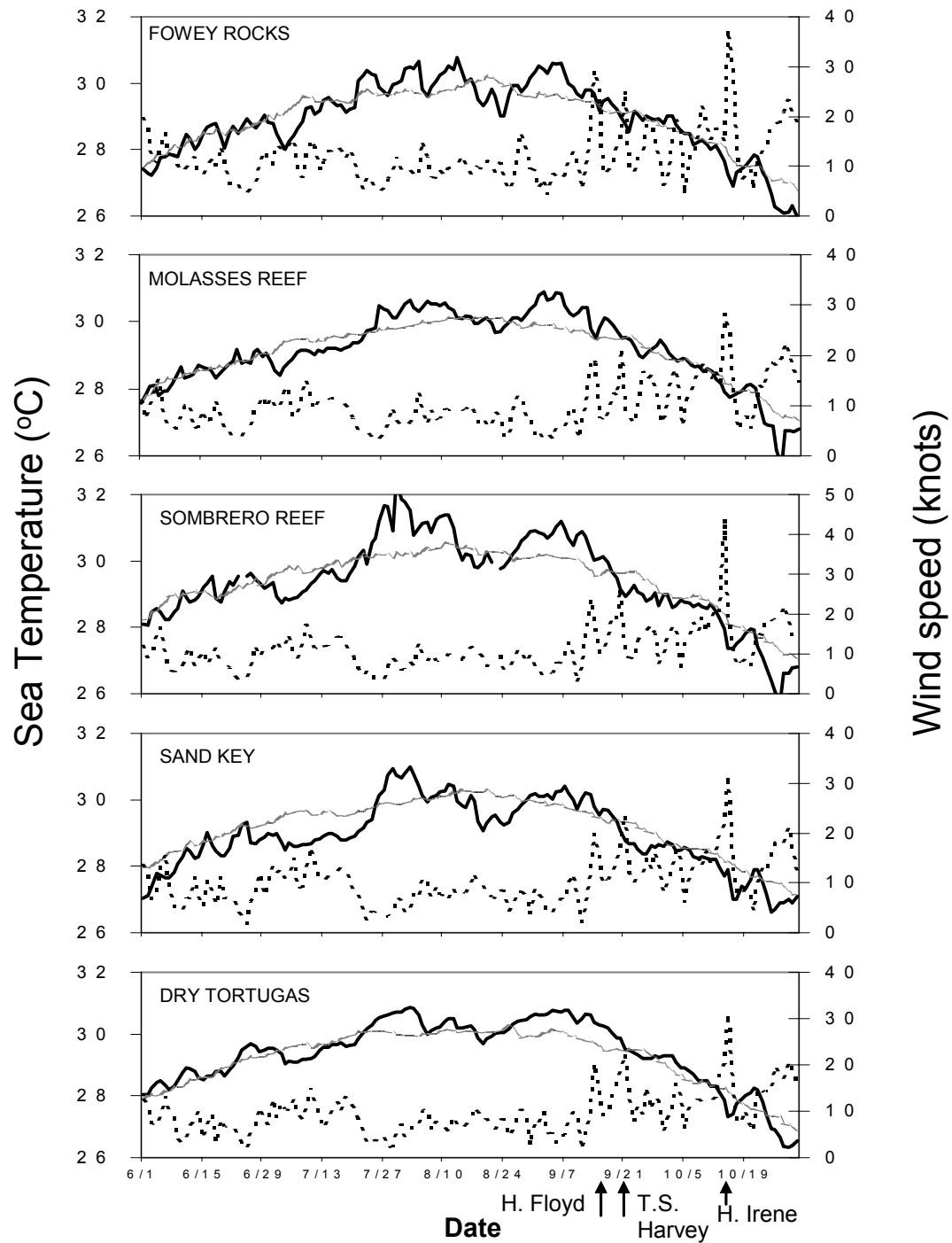
Figure 2.2. Daily average of hourly sea temperature (solid line) and wind speed (dashed line) for sites located along the Florida Reef Tract from 1 June 1999 – 31 October 1999. Shaded line is the seasonal cycle for sea temperature.
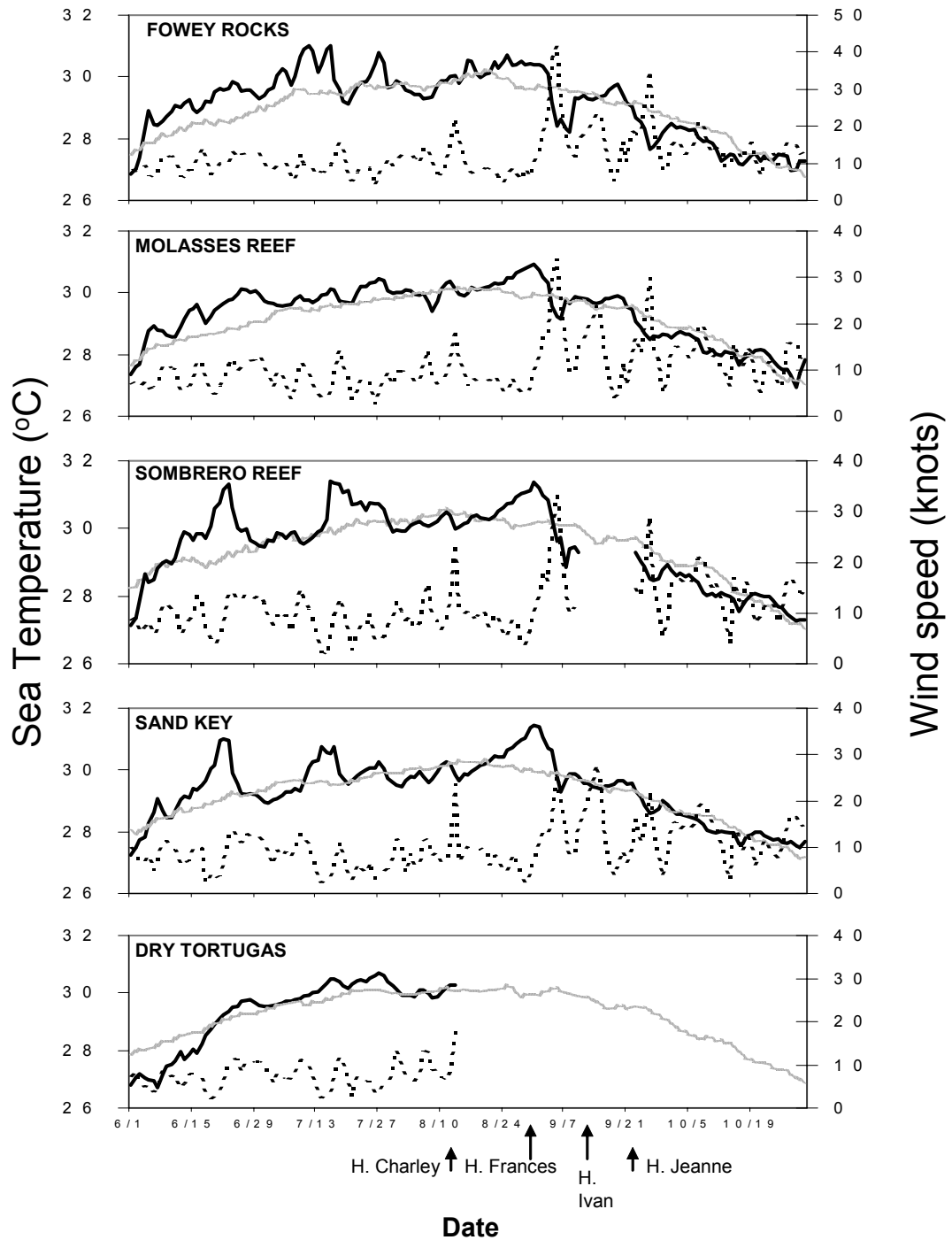
Figure 2.3. Daily average sea temperature (solid line) and wind speed (dashed line) for sites located along the Florida Reef Tract from 1 June – 31 October 2004. Shaded line is the seasonal cycle for sea temperature. Hurricane Charley disabled station at Dry Tortugas.
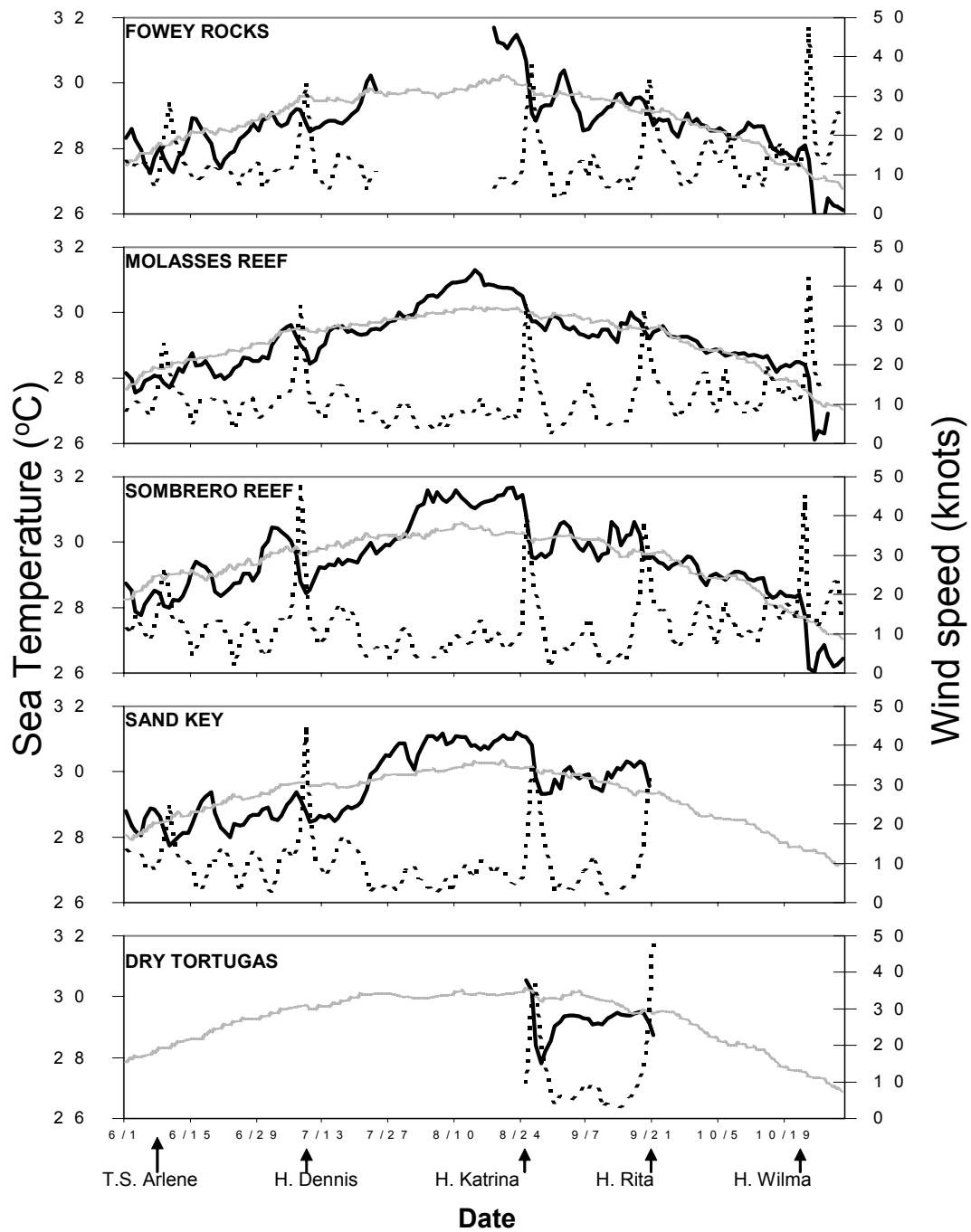
Figure 2.4. Daily average sea temperature (solid line) and wind speed (dashed line) for sites on the Florida Reef Tract from 1 June – 31 October 2005. Shaded line is the seasonal cycle for sea temperature. Hurricane Rita disabled stations at Sand Key and Dry Tortugas.

The duration of sea temperature decrease to levels below average ranged from 1 – 40 days (mean ± s.e.m. = 11 days ± 1.2, n = 49) for storms within 400 km, and from 0 - 6 days for storms > 400 km from reef sites on the Florida Reef Tract (mean ± s.e.m. = 2 days ± 0.9, n = 10) (Table 2.3).   The duration of cooling was significantly related to $\Delta^{\circ}C$ (correlation analysis, r = 0.49, n = 59, p < 0.0001), distance from the storm track and wind speed (Table 2.2). Unlike $\Delta^{\circ}C$, the duration of cooling was not significantly related to the side of storm passage (Table 2.2).

Discussion

The magnitude of cooling reported is consistent with observations made in Okinawa (Glynn, 1996; Nadaoka *et al.*, 2001). The most intense surface seawater cooling in the open ocean occurs to the right of a storm's track in the Northern hemisphere (Cornillion *et al*., 1987; Price *et al*., 1994; Xie *et al*., 1998; Price, 1981; Stramma *et al*., 1996), but the dynamics of hurricane-induced cooling for reef sites, and complex coastal and shelf environments, are poorly understood (Xie *et al*., 1998). Glynn (1996) found that the magnitude of cooling on Okinawan reefs from typhoon passage was not dependent on the side of storm passage. In this study, greater cooling occurred to the left of the storm track. These results suggest that the coastal cooling response may differ from that in the open ocean.

Approximately 81 hurricanes have made landfall in either southeast or southwest Florida from 1851-2005 ($f_{hurricane-(1851-2005)}$ = 0.53 hurricanes yr^{-1}) (Jarrell *et al*., 2001; Landsea, 2007), whereas five widespread coral bleaching events have impacted the Florida Reef Tract from 1987 to 2005 ($f_{bleaching-(1987-2005)}$ = 0.26 events yr^{-1}) (Causey, 2001). If we use these frequencies as a baseline for the expected rate of

future events, we find that the chance of a hurricane landfall and a bleaching event co-

occurring in any given year is low ($p = 0.14$). If we assume the rate of bleaching in

Table 2.2. *F*-statistics, *p*-values, and r^2 for linear regression and ANCOVA tests of the relationship between Δ^oC and duration of cooling with distance from storm center, wind speed, and side of storm passage (left or right). ANCOVA tests represent results from test for equal slopes as all tests for unequal slopes were not significant.

	Δ^oC			Duration of cooling		
	F	r^2	*p*-value	*F*	r^2	*p*-value
Distance	24.4	0.29	< 0.0001	14.0	0.20	0.0001
Wind speed	22.6	0.27	< 0.0001	12.4	0.18	0.001
Side of passage	5.8	0.09	0.01	0.19	0.003	ns
Distance * side of passage	19.9	0.40	< 0.0001	7.1	0.20	0.001
Wind * side of passage	17.9	0.37	< 0.0001	6.3	0.18	0.001

Δ^oC was log transformed [ln (Δ^oC)] and duration of cooling was square root transformed for regression analyses.

the future will be more representative of that observed from 1997 to 2005 ($f_{bleaching-(1997-2005)} = 0.33$ yr^{-1}), the probability of these two phenomena co-occurring in the

same year increases slightly ($p = f_{bleaching-(1997-2005)} \cdot f_{hurricane-(1851-2005)} = 0.17$). The

benefit that temperature-stressed corals may derive from proximal hurricane passage

increases proportionally with the number of hurricanes in a given year, but multiple

hurricane impacts at the same site in one year becomes less likely with each additional

storm. For instance, the likelihood of four hurricanes impacting the Florida Reef

Tract, which occurred in 2005, coincident with a bleaching event is rare ($p = 0.02$).

The factors conducive to coral bleaching and hurricane formation are not entirely

independent [*i.e.*, warm water, low vertical wind shear (Landsea, 2007)] and the

historical data of hurricane events only considers storms that made landfall in south

Florida. Hurricanes Dennis and Rita did not make landfall in south Florida in 2005,

Table 2.3. Duration (days: max., min.) of cooling associated with named storms that
affected the Florida Reef Tract from 1998-2005.

		Max. duration of cooling	Min. duration of cooling
Year	Storm name	Value (Site)	Value (Site)
1998	H Georges	9 (MR*, SK*)	7 (FR, SR)
1999	H Floyd	1 (FR)	0 (MR, SR, SK, DT)
1999	TS Harvey	12 (SK)	3 (FR)
1999	H Irene	9 (FR)	5 (MR)
2001	TS Gabrielle	15 (FR)	2 (SR)
2001	H Michelle	40 (MR)	5 (SR)
2004	H Charley	7 (SK)	1 (FR)
2004	H Frances	11 (FR)	3 (MR, SK)
2004	H Ivan	5 (SK)	0 (FR, MR)
2004	H Jeanne	26 (FR)	5 (SK)
2005	TS Arlene	8 (SK)	4 (MR*)
2005	H Dennis	23 (SR)	8 (MR)
2005	H Katrina	21 (DT)	4 (FR)
2005	H Rita	8 (FR)	3 (MR)
2005	H Wilma	22 (FR)	11 (SR)

*Indicates that site was below long-term average before impact of storm. Value refers to number of
days it took for sea temperature to warm to pre-storm value.

yet cooling along the entire Florida Reef Tract was observed as a result of these storms (Table 2.1). Thus, these factors likely make the probabilities reported an underestimate of the chances of these two events occurring at the same time.

Conclusions

Hurricane cooling is not expected to nullify the proposed effects of climate change on coral reefs (*e.g.*, Hoegh-Guldberg, 1999; Hughes *et al*., 2003); however, instances in which hurricane and bleaching events co-occur can have a significant effect on coral reef persistence. The area of cooling extends substantially outside the narrow swath of physical damage providing empirical evidence that the passage of a hurricane can proportionally benefit a much greater area than it disturbs when reef corals are thermally stressed. During the 2005 Caribbean-wide bleaching event, the Florida Reef Tract was impacted by multiple hurricanes, whereas no major storms passed within 400 km of the US Virgin Islands (USVI). Consequently, the prevalence of bleaching was considerably less and recovery occurred more rapidly on Florida reefs compared to those in the USVI (Manzello *et al.*, 2007). Hurricane-induced cooling on Florida reefs depressed the accumulation of thermal stress, which likely explains the differences in bleaching between Florida and the USVI (Fig. 2.5). Single, severe bleaching events can have dramatic, long-lasting impacts on the structure and function of coral reefs (Glynn, 1988) and the cooling benefit of a hurricane can have substantial mitigative effects as documented in this study (Fig. 2.6).
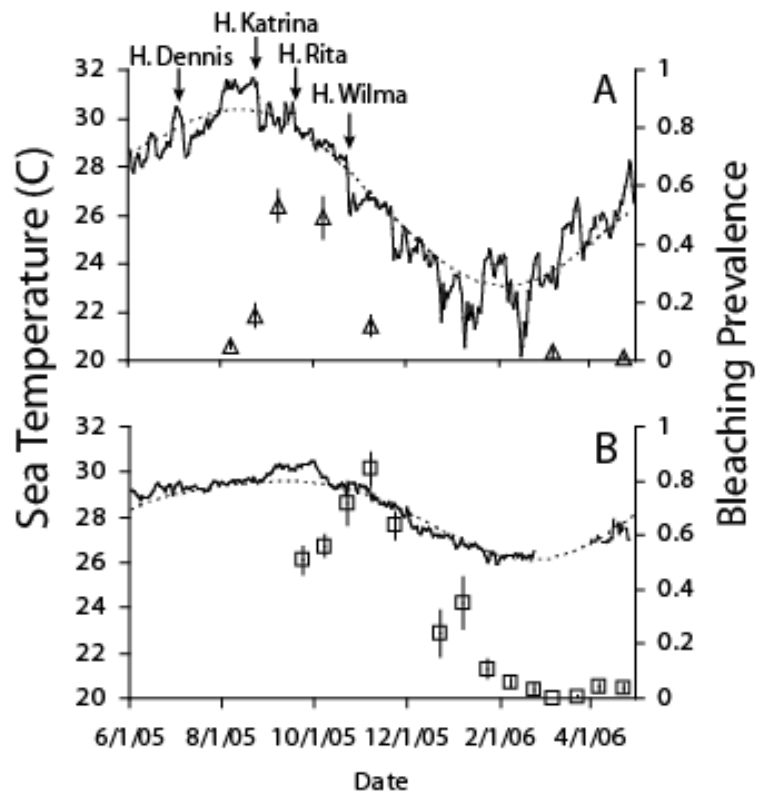
Figure 2.5. Daily average sea temperature and bleaching prevalence from June 2005 through April 2006. (A) Florida Reef Tract. (B) US Virgin Islands. Data points represent mean ± s.e.m bleaching prevalence. Solid and dashed lines represent the daily average and seasonal cycle for sea temperature, respectively. Arrows indicate timing of hurricane impacts clearly showing the cooling effect. © *PNAS*
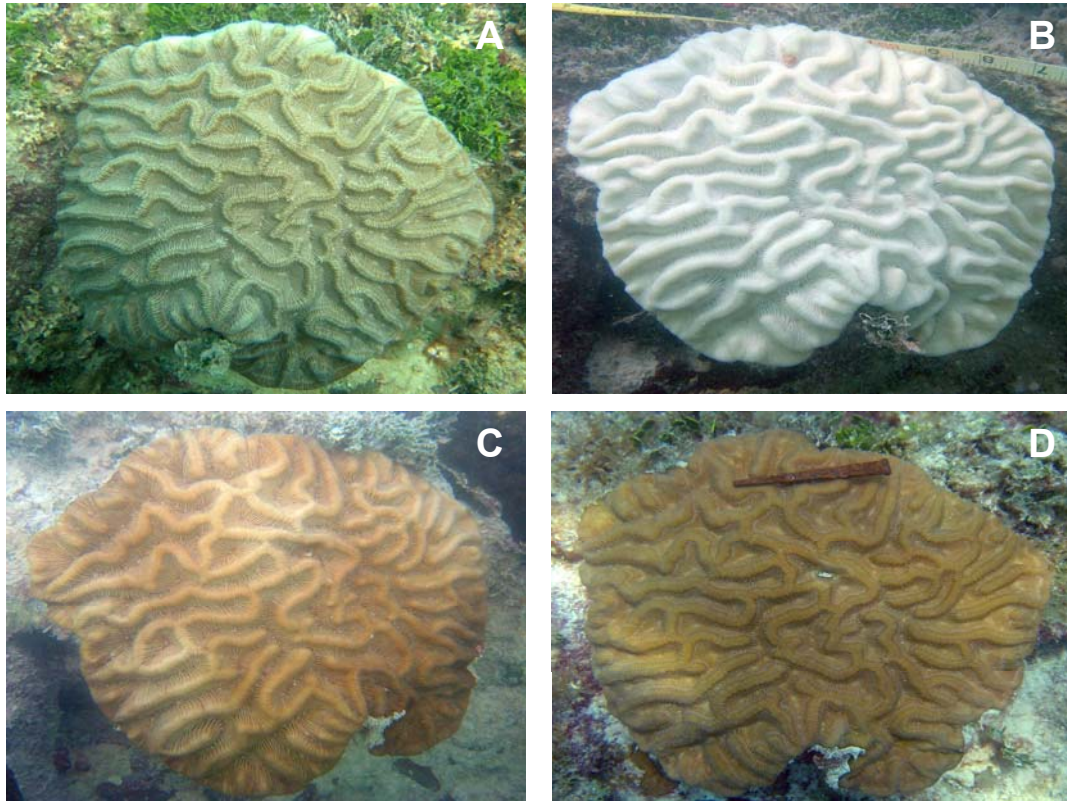
Figure 2.6. Time-series of bleached coral (*Colpophyllia natans*) at Coral Gardens, Florida Reef Tract. (A) Pre-bleaching (11 Aug. 2005). (B) Bleached (6 Sept. 2005). (C) nearly recovered (9 Nov. 2005). (D) Recovered with normal pigmentation (2 Mar. 2006). Nail in photograph (D) is 8.3 cm in length. © *PNAS*

Chapter 3: CO$_2$ variability of surface waters from eastern tropical Pacific coral reef sites in Galápagos and Panamá

Ocean Acidification

An estimated one-third of all the CO$_2$ released into the atmosphere since the industrial revolution has been absorbed by the oceans (Feely *et al*., 2004; Sabine *et al*., 2004). This ongoing and accelerating uptake of atmospheric CO$_2$ is causing a drop in seawater pH at the global scale (Orr *et al*., 2005), resulting in an acidification of the surface ocean (Caldeira and Wickett, 2003). Ocean acidification results in a decrease in seawater [CO$_3^{2-}$] and, consequently, a decrease in the saturation state (Ω) of carbonate minerals (Ω = [CO$_3^{2-}$][Ca^{2+}]/K$'_{sp}$, where K$'_{sp}$ is the solubility product for a carbonate mineral (e.g., aragonite, calcite); see review by Kleypas *et al*., 2006). Acidification is expected to reduce coral reef calcification and increase reef dissolution, and the relative rates of change will likely be a function of pCO$_2$ (the partial pressure of CO$_2$) in surface seawater, which is near equilibrium with pCO$_2$ in the atmosphere (Smith and Buddemeier, 1992; Kleypas *et al*., 1999; Langdon *et al*., 2000; Yates and Halley, 2006). Carbonate budget studies have shown that healthy coral reefs exhibit low net accretion due to high rates of physical, chemical and biological erosion (see review by Glynn, 1997). Consequently, any disturbance that causes either decreased accretion or increased erosion may tip the tenuous balance from reef framework growth to loss.

There have been a limited number of field measurements to determine seawater carbonate chemistry for coral reef waters. Short-term field studies have investigated the carbonate chemistry of coral reef waters in Japan (Kayanne *et al*., 1995; Suzuki *et al*., 1995; Ohde and Van Woesik, 1999), Moorea (Gattuso *et al*., 1993), at the Palau Barrier Reef and Majuro Atoll (Kawahata *et al*., 1997), the Great

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Barrier Reef (Suzuki *et al*., 2001, 2003), and Bermuda (Bates, 2002).   Only two long-term, time-series measurements of carbonate chemistry exist: The Hawaiian Ocean Time-Series (HOT) and the Bermuda-Atlantic Time-Series (BATS) (Bates, 2001; Gruber *et al*., 2002; Brix *et al*., 2004), albeit these measurements are taken in oceanic waters at a considerable distance from coral reefs. Therefore, there is a need for long-term sampling (*i.e.*, multiple years) of the carbonate system from reef waters.

Surface waters in many parts of the eastern tropical Pacific (ETP) have lower pH, lower Ω, and higher pCO_2 values relative to the rest of the tropics because CO_2-enriched deep waters are upwelled to the surface layers along the shallow thermocline (Fig. 3.1) (see review by Millero, 2007). The intensity of this upwelling varies regionally and strongly influences reef development across the ETP (reviewed by Cortés, 1997).   Three well-studied ETP coral reef areas with contrasting oceanographic environments were chosen for study in the Galápagos Islands and Pacific Panamá. The Galápagos Islands are located where the Peru Current meets and mixes with the warmer tropical surface water mass from the north creating the equatorial front. The equatorial front migrates seasonally, but can be generally characterized as having sea surface temperatures (SST) ranging from 20 to 24°C and salinities from 33.5 to 35.0 (Glynn, 2003). These oceanographic conditions are representative of those that influence existing coral communities in the Galápagos (Fig. 3.2A). Two separate gulfs with differing physical characteristics occur off the coast of Pacific Panamá: the Gulf of Chiriquí and Gulf of Panamá (Fig. 3.3). Both gulfs experience a wet and dry season that is controlled by the position of the Intertropical Convergence Zone (Glynn and Maté, 1997).   During the wet season (end of April to mid-December), oceanographic conditions in the surface layers are similar in both gulfs with SSTs ranging from 27.5 to 29°C and salinities from 29.5 to

33.5 (Glynn and Maté, 1997; D'Croz and O'Dea, 2007) (Fig. 3.2A).   In the dry

season (mid-December to the end of April), the Gulf of Panamá experiences

upwelling because surface waters are advected offshore by the funneling of the NE

tradewinds through the low-lying Isthmus of eastern Panamá. During upwelling in

the Gulf of Panamá, SST decreases to 18-24°C, whereas salinities increase to > 33

(Glynn and Maté, 1997) (Fig. 3.2A).   The Gulf of Chiriquí does not experience

classical upwelling because the mountainous topography of western, mainland

Panamá blocks the flow of the NE tradewinds; impeding the advection of surface

waters offshore [see D'Croz and O'Dea (2007) and refs. cited therein].   Although

traditional upwelling does not occur in the Gulf of Chiriquí, increased wind force in

the dry season causes measurable shoaling of the already shallow thermocline to

shallow depths of 5-15 m (Fig. 3.2B) (Dana, 1975). Recent observations suggest that

thermocline shoaling may be more common in the Gulf of Chiriquí than was

previously appreciated (D'Croz and O'Dea, 2007).
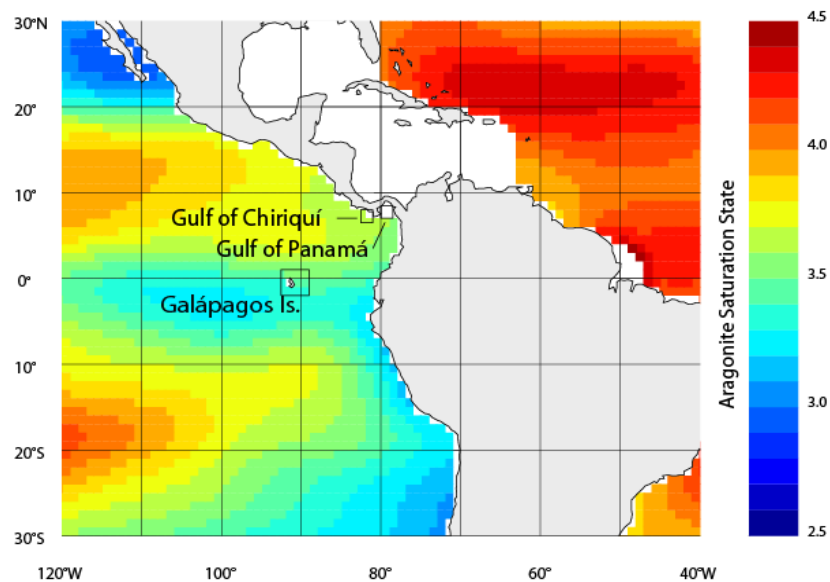
Figure 3.1. Map showing depressed aragonite saturation state (Ω_{arag}) across eastern tropical Pacific in comparison to highly supersaturated waters that influence Caribbean reef sites. Aragonite is the form of $CaCO_3$ secreted by reef-building corals.

Regardless of the nature of the upwelling, the Ω of the surface layers in the ETP is strongly influenced by sub-thermocline waters. This is further illustrated by the fact that the pCO_2 of most surface waters in the ETP is higher than atmospheric pCO_2 (*i.e.*, pCO_2 of surface waters is > atmospheric pCO_2: see Takahashi *et al.*, 1997). For comparison, the Ω of tropical surface waters in nonupwelling regions of the globe are near equilibrium with and controlled by the atmospheric concentration of CO_2 (Kleypas *et al.*, 1999).
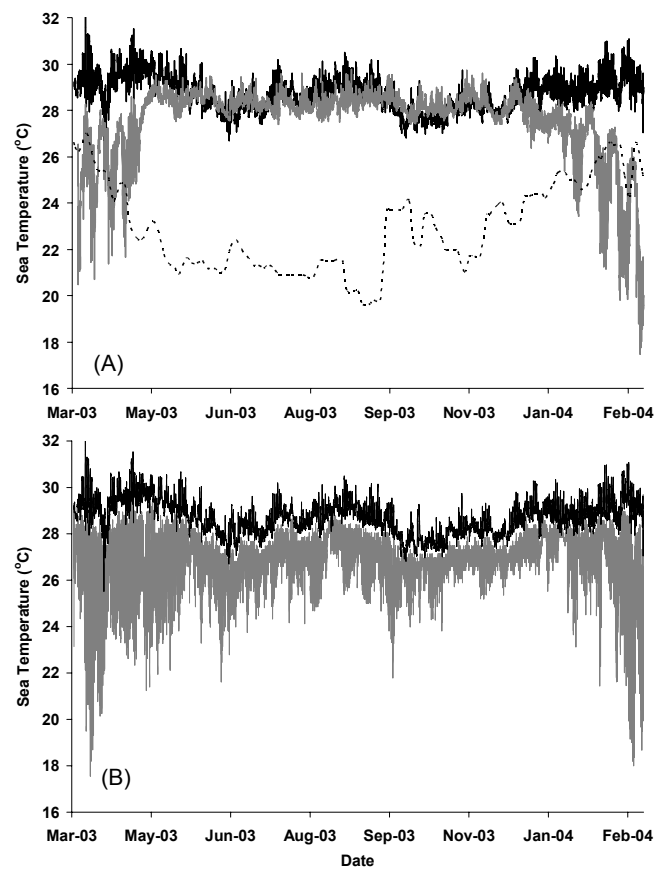
Figure 3.2. Time-series of sea temperature from: (A) Uva Reef, Panamá (black line, ~1 m MLW), Saboga Reef, Panamá (gray line, ~1 m MLW), and Galápagos (dashed line, SST); (B) Uva Reef flat (~1 m) and 15 m depth (gray line) showing high variance in temperature at depth to illustrate apparent shoaling of shallow thermocline. Galapagos SST obtained from:
http://coralreefwatch.noaa.gov/satellite/current/sst_series_24reefs.html

Extensive and near-annual monitoring of the physical and biological conditions at the Uva reef in Pacific Panamá was initiated in the early 1970s by P. W. Glynn and colleagues. This long-term record (> 30 yrs) of reef-building coral populations and communities is a cornerstone to the current state of knowledge on coral and coral reef response to elevated seawater temperatures (see Glynn *et al*., 2001 and references cited therein). Consequently, the role of thermal stress in coral bleaching has been extensively studied for eastern Pacific coral reefs (Podesta and Glynn, 1997, 2001), whereas the chemical ramifications of climate change have yet to be considered. Therefore, the Uva Reef, and perhaps the entire ETP, may be an exemplary natural laboratory for study of the combined thermal and chemical impacts of global change. To gauge potential change, we must first establish baseline conditions. Seawater carbonate chemistry was analyzed from discrete samples taken over several years from the ETP reef sites.

Methods

Seawater samples were collected in 500 ml borosilicate glass bottles via SCUBA from the Uva Reef (Pacific Panamá, Gulf of Chiriquí) during three wet (September 2003 and 2006, August 2007) and three dry seasons (March 2004, 2005, 2006) and also from five 'former' reef sites in the Galápagos Islands in May 2003 (Fig. 3.3: see Glynn and Wellington (1983) for description of Galápagos coral reef sites prior to 1982-83 El Niño-Southern Oscillation (ENSO) warming event). Modest sampling ($n = 12$, March 2005) was performed during an upwelling pulse (dry season) and also during the non-upwelling wet season ($n = 12$, August 2007) on the Saboga Reef in the Gulf of Panamá (Fig. 3.3). All seawater samples were immediately preserved with ~200 μl of saturated $HgCl_2$ solution to halt biological activity. Seawater temperature at the time of sampling in Panamá was obtained from an *in situ*
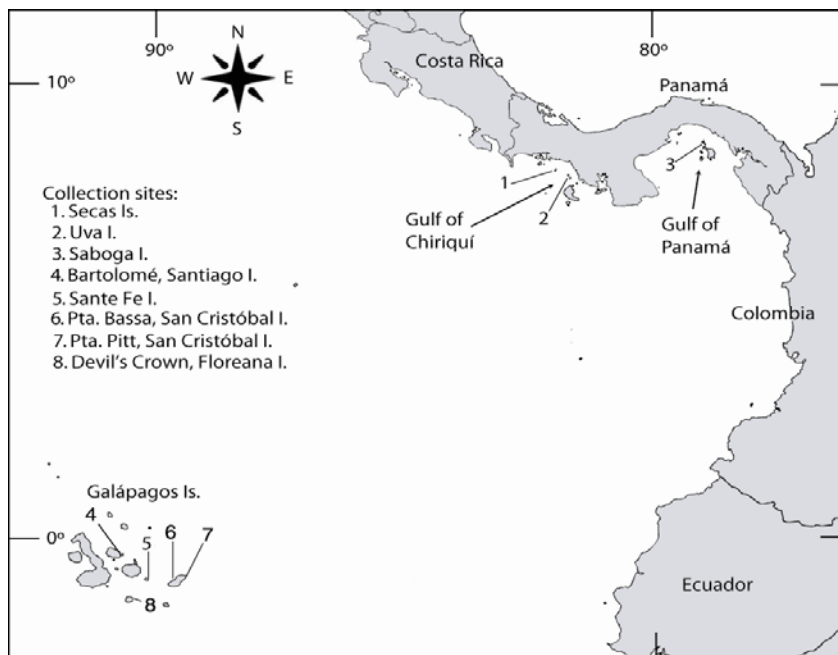
Figure 3.3. Map of eastern tropical Pacific indicating location of reefs sampled. Numbers denote reefs at (1) Secas Is. (7° 57'18"N; 82° 00'45"W), (2) Uva I. (7° 48'48"N; 81° 45'32"W), (3) Saboga I. (8° 37'43"N; 79° 03'26"W), (4) Bartolomé, Santiago I. ($0°$ 17'17"S; $90°$ 33'15"W), (5) Sante Fe I. (0° 48'17"S; 90° 2'20"W), (6) P. Bassa (0° 49'N; 89° 32'W) and (7) Punta Pitt (0° 42'30"S; 89° 15'W), San Cristóbal I., and (8) Devil's Crown, Floreana I. ($1°$ 12'59"S; $90°$ 25'23"W).

HOBO (Onset Corp.) thermistor fixed on the reef that logged temperature every half hour. TCO_2 was measured coulometrically (Chipman *et al*., 1993) with a SOMMA system, whereas TA was determined using a gran titration *sensu* Langdon *et al*. (2000). Duplicate samples were taken in Panamá (*n* = 25 pairs) and the Galápagos Islands (*n* = 5 pairs) and paired *t*-tests showed that preservation did not differ between duplicate samples as values for TCO_2 and TA of duplicates normalized to salinity were not statistically different (*p* >>0.1). Measurement of TA and TCO_2 allowed the calculation of seawater pCO_2, pH and Ω_{arag} (Millero, 1979). The carbonate parameters (pCO_2, pH and Ω_{arag}) were calculated with the CO2SYS computer program (Lewis and Wallace, 1998) using the dissociation constants of Mehrbach *et*

al. (1973) for carbonic acid as refit by Dickson and Millero (1987), and Dickson (1990) for boric acid. Ω_{arag} was calculated according to Mucci (1983).

The nonparametric Mann-Whitney *U*-test was used for statistical comparisons between two sites, whereas the Kruskal-Wallis one-way ANOVA (nonparametric) was used when more than two sites were compared. An alpha level of 0.05 was used for significance in all statistical tests.

Results

CO$_2$ variability across eastern tropical Pacific reef sites

Temperature, salinity, Total CO$_2$ (TCO$_2$), total alkalinity (TA), pH, pCO$_2$ and Ω_{arag} values were significantly different across the ETP sites (Kruskal-Wallis test, *p* < 0.0001) (Table 3.1). Salinity, TCO$_2$, TA, and pCO$_2$ values were significantly greater, whereas temperature, pH and Ω_{arag} values were significantly lower in the Galápagos Islands compared to the Panamá sites (Mann-Whitney *U*-tests, *p* < 0.0001 for all tests) (Fig. 3.4). Values of TA were no different between ETP sites when normalized to salinity (nTA: Kruskal-Wallis test, χ^2 = 0.7, df = 2, *p* >> 0.1); however nTCO$_2$ values were still different (Kruskal-Wallis test, χ^2 = 61.2, df = 2, *p* < 0.0001).

CO$_2$ variability within Panamá sites

Salinity, TCO$_2$, TA, and pCO$_2$ were significantly higher during the dry season in both gulfs illustrating the effect of seasonal upwelling (Tables 3.1 and 3.2). Temperature was stable year-round in the surface layers of the Gulf of Chiriquí, but was significantly depressed in the Gulf of Panamá during the dry season (Fig. 3.2A, Table 3.2A). Ω_{arag} values were lower in the dry season in both gulfs (Table 3.1), but this difference was only significant in the Gulf of Panamá (Table 3.2A). In the Gulf of Chiriquí, pH was significantly depressed in the dry season, but was no different in the Gulf of Panamá (Table 3.1, 3.2A).

Table 3.1. Measured geochemical variables for ETP reef sites compared to estimated average values for the tropical surface ocean (TSO) under preindustrial and a doubling of atmospheric CO_2. Values represent means (± standard error of the mean). Estimated values were calculated by combining SST, salinity, and PO_4 from the 2005 World Ocean Atlas (Boyer *et al*., 2006) with total carbon dioxide (TCO_2) and total alkalinity (TA) values from the 1x1 degree gridded GLODAP data (Sabine *et al*., 2005). TSO averages were determined for waters between 30ºN and 30ºS. Preindustrial and $2xCO_2$ values were estimated by assuming 1990s values for salinity, PO_4, SiO_2 and TA, and adjusting SST and TCO_2 in accordance with future climate projections.

Location	Data description	Year (s)	n	Salinity	TCO_2 (μmol kg^{-1})	TA (μeq kg^{-1})	pH (sws)	pCO_2 (μatm)	Ω_{arag}
Galápagos[*]	Field data	2003	23	35.1 (0.01)	2091.2 (5.27)	2299.3 (5.39)	7.88 (0.02)	636 (25.4)	2.49 (0.07)
Panamá-G. of Panamá[†] (Saboga Reef)	Field data – Dry Season: Upwelling	2005	12	33.4 (0.04)	1932.7 (8.02)	2176.6 (7.0)	8.01 (0.01)	422 (11.70)	2.79 (0.05)
Panamá-G. of Panamá[†] (Saboga Reef)	Field data – Wet Season: Nonupwelling	2007	12	28.4 (0.09)	1624.3 (5.79)	1869.5 (1.51)	8.01 (0.01)	368 (11.57)	2.96 (0.06)
Panamá-G. of Chiriquí[‡] (Uva Reef)	Field data – Dry Season: Increased shoaling of thermocline	2004, 2005, 2006	46	33.1 (0.05)	1851.6 (8.53)	2145.3 (6.92)	7.98 (0.02)	447 (22.2)	3.50 (0.09)
Panamá-G. of Chiriquí[‡] (Uva Reef)	Field data – Wet Season: Nonupwelling	2003, 2006, 2007	36	30.5 (0.08)	1723.3 (8.40)	2018.5 (6.30)	8.04 (0.01)	353 (10.3)	3.53 (0.08)
Tropical surface ocean[§]	Estimated	1880 (*pre-ind.*)	-	35.1	1930	2315	8.16	280	4.3
Tropical surface ocean[§]	Estimated	1990s	-	35.1	1969	2315	8.09	340	3.8
Tropical surface ocean[§]	Estimated	*2 x CO$_2$*	-	35.1	2061	2315	7.91	560	3.0

[*]Average SST and nutrient concentrations (PO_4 = 0.6 μM, SiO_2 = 4.8 μM) measured in surface layers (0-5 m) near Galápagos Is. over period 1980-2005 (Pennington *et al*., 2006) were used for CO_2 calculations.

[†]CO_2 calculations for Saboga Reef in 2005 (n = 12, during upwelling pulse) all use 21ºC because *in situ* temperature data were unavailable. Twenty-one degrees Celsius was considered an approximate modal SST for these upwelling pulses [Range: 16 – 24ºC (D'Croz and O'Dea, 2007)]. Bi-annual nutrient concentrations were used for CO_2 calculations because of the effect of seasonal upwelling on these values [Dry season (upwelling): PO_4 = 0.83 μM, SiO_2 = 8.93 μM; Wet Season (nonupwelling): PO_4 = 0.21 μM, SiO_2 = 3.61 μM (D'Croz and O'Dea, 2007)].

[‡] Annual mean nutrient concentrations measured in surface layer [< 20 m: PO_4 = 0.19 μM, SiO_2 = 4.55 μM (D'Croz and O'Dea, 2007)] were used for CO_2 calculations as nutrient values did not differ significantly across seasons for the Gulf of Chiriquí.

[§]Nutrient concentrations of average tropical surface ocean water were PO_4 = 0.23 μM, SiO_2 = 2.28 μM (Boyer *et al*., 2006).
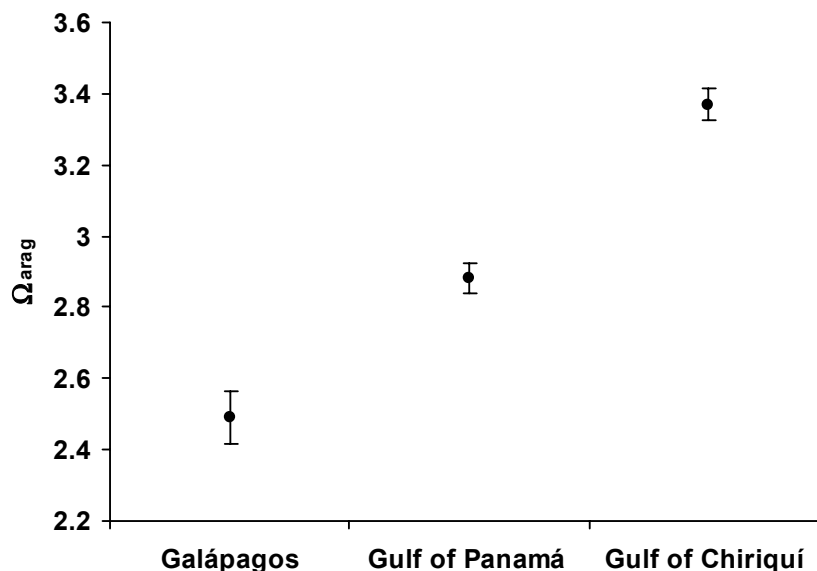
Figure 3.4. Saturation state of aragonite (Ω_{arag}) measured in surface waters from reef sites in Galápagos, Gulf of Panamá, and Gulf of Chiriquí. Values represent means ± standard error of the mean.

CO_2 variability between Panamá sites

Salinity, TCO_2, TA, pH and pCO_2 were no different between Panamanian gulfs when data were pooled by site and season was ignored (Table 3.2B). Temperature was significantly greater in the Gulf of Chiriquí when the data were pooled. Ω_{arag} values were significantly lower in the Gulf of Panamá relative to the Gulf of Chiriquí regardless of season (Table 3.1, 3.2B). During the upwelling dry season, salinity and TCO_2 values were significantly higher, but temperature and Ω_{arag} were significantly lower in the Gulf of Panamá compared to the Gulf of Chiriquí (Table 3.1, 3.2B). TA, pH and pCO_2 were no different between gulfs in the dry season (Table 3.2B). This suggests that the chemical signature of upwelled waters is similar across gulfs and the differences reported herein appear to solely reflect the

Table 3.2. Relevant statistics of Mann-Whitney U-tests* comparing seasonal differences in geochemical and environmental variables (A) within and (B) between Panamá sites. U is the calculated Mann-Whitney statistic and p is probability that the two distributions are not significantly different.

Wet vs. dry season
(A) Within sites

Variable	Gulf of Chiriquí		Gulf of Panamá	
	U	p	U	p
Temperature	3694	ns	222	< 0.001
Salinity	1786.5	< 0.001	78	< 0.00
TCO_2	2064.5	< 0.001	78	< 0.001
TA	1895	< 0.01	78	< 0.001
pH	4358.8	ns	151	ns
pCO_2	3204	< 0.01	103	< 0.01
Ω_{arag}	3384.5	< 0.05	185.5	< 0.05

(B) Between sites

Variable	Pooled data		Wet Season		Dry Season	
	U	p	U	p	U	p
Temperature	1290	< 0.01	584	< 0.05	78	< 0.001
Salinity	1689	ns	79	< 0.001	770	< 0.01
TCO_2	1772	ns	98	< 0.001	848	< 0.001
TA	1584	ns	78	< 0.001	671	ns
pH	2204	ns	444	ns	665.5	ns
pCO_2	1568	ns	320	ns	464	ns
Ω_{arag}	796	< 0.01	229	< 0.01	184.5	< 0.01

*Statistical comparisons performed on measured and/or inferred values from discrete samples and do not represent time-series analysis.

greater intensity of upwelling in the Gulf of Panamá. During the nonupwelling wet season, salinity, TCO_2, TA, and Ω_{arag} were significantly depressed in the Gulf of Panamá relative to the Gulf of Chiriquí (Table 3.1, 3.2B). However, pCO_2 and pH were no different between the Gulf of Panamá and Gulf of Chiriquí during this time (Table 3.2B) showing that wet season differences between Panamanian gulfs reflects differential freshwater dilution of the surface layers. A decline in salinity of 5 would correspond with a decline in Ω_{arag} of up to 0.7 because of the lowered $[Ca^{2+}]$. Thus, the ~0.3 lower Ω_{arag} in the Gulf of Panamá mainly reflects the lower salinity there (Table 3.1). Temperature was slightly warmer in the Gulf of Panamá relative to the Gulf of Chiriquí during the wet season (Mann-Whitney U-test, $p < 0.05$). This is likely just an artifact of the small sample size from the Gulf of Panamá ($n = 12$, Table

3.1) as more thorough studies have demonstrated that thermal conditions across both gulfs are no different during the wet season (*e.g.*, D'Croz and O'Dea, 2007).

Table 3.3. Mean (± standard error of the mean) values of TCO_2, TA, pH, pCO_2, and Ω_{arag} measured at the Uva Reef in the Gulf of Chiriquí, Panamá during wet and dry seasons.

Season		*n*	TCO_2	TA	pH	pCO_2	Ω_{arag}
Dry		68	1860.2 (6.2)	2151.4 (5.3)	7.98 (0.011)	448 (15.7)	3.47 (0.07)
	Day	46	1851.6 (8.5)	2145.3 (6.9)	7.98 (0.015)	447 (22.2)	3.50 (0.09)
	Night	22	1878.3 (5.7)	2164.1 (6.9)	7.97 (0.013)	449 (15.1)	3.41 (0.10)
Wet		53	1740.3 (6.9)	2017.9 (5.0)	8.01 (0.011)	388 (10.8)	3.34 (0.07)
	Day	36	1723.3 (8.4)	2018.5 (6.3)	8.04 (0.012)	353 (10.3)	3.53 (0.08)
	Night	17	1776.3 (6.5)	2016.7 (8.1)	7.95 (0.046)	462 (13.9)	2.94 (0.06)

CO₂ temporal variability at Uva Reef

TCO_2 was significantly greater at night in both wet and dry seasons (Mann-Whitney *U*-test, $p < 0.05$ for both tests). TA was significantly greater at night in the dry season, but no diel differences were observed in the wet season ($p < 0.05$ and $\gg$ 0.1, respectively; Table 3.3). The remaining carbonate parameters (*i.e.*, pH, pCO_2, Ω_{arag}) were no different between night and day within the dry season ($p > 0.1$ for all tests). In the wet season, pCO_2 values were significantly greater, whereas pH and Ω_{arag} values were significantly depressed at night relative to those measured during the day (Mann-Whitney *U*-test, $p < 0.0001$ for all tests, Table 3.3). Salinity normalized values of TCO2 and TA are presented in Table 3.4.

CO₂ spatial variability at Uva Reef

Deep waters (*i.e.*, ~15 m) had significantly higher TCO_2 and TA relative to surface waters across all seasons (Tables 3.5 and 3.6). nTA values were significantly greater at depth during the dry seasons, but not during the wet season (Table 3.4).

Table 3.4. TCO_2 and TA values salinity normalized at Uva Reef during wet and dry seasons. Values represent means ($\pm$ sem)

Season		n	$nTCO_2$	nTA
Dry		68	1969.2 (6.11)	2277.5 (5.21)
	Day	46	1957.6 (8.14)	2268.3 (6.69)
	Night	22	1993.4 (5.46)	2296.6 (6.41)
Wet		53	1999.2 (6.67)	2318.3 (5.02)
	Day	36	1979.3 (7.34)	2318.6 (6.05)
	Night	17	2041.2 (6.26)	2317.5 (9.27)

Conversely, pH values were significantly lower at depth during the wet season, but not during the dry season (Table 3.5). Values of pCO_2 were significantly greater at depth in both the wet and dry seasons, albeit this difference was more significant in the wet season. Ω_{arag} values were significantly depressed at depth in both seasons, but this difference was more significant in the dry season.

Table 3.5. Comparison of mean ($\pm$ sem) carbonate parameters of surface seawater from that at depth at the Uva Reef.

Location	n	TCO_2	TA	pH	pCO_2	Ω_{arag}
Surface < 5 m	82	1795.3 (9.27)	2089.6 (8.45)	8.01 (0.01)	406 (14.1)	3.51 (0.06)
~15 m	13	1931.0 (18.8)	2187.5 (15.4)	7.96 (0.012)	480 (16.5)	3.05 (0.09)

For pooled data: $n_{surface} = 82$, $n_{15m} = 13$; Wet season data: $n_{surface} = 36$, $n_{15m} = 5$; Dry season data: $n_{surface} = 46$, $n_{15m} = 8$

Discussion

The ranges of the carbonate parameters (Ω_{arag}, pCO_2, and pH) across the ETP sites studied are representative of the expected changes in global surface seawater with a doubling of atmospheric CO_2 (Table 3.1) (Kleypas *et al*., 1999). The Ω_{arag} values documented in Galápagos were lower than what is expected throughout the tropics at the end of this century with an excess of double the preindustrial

atmospheric CO_2 levels, whereas Ω_{arag} values measured in the Gulf of Panamá were similar to this value. The highest Ω_{arag} values documented in this study occur in the Gulf of Chiriquí, which corresponds with the greatest reef development and highest coral species diversity of the entire ETP (Fig. 3.5) (Glynn *et al.*, 1972; Dana, 1975; Glynn and Maté, 1997). The fact that Ω_{arag} values documented at the ETP reef sites (Table 3.1) were lower than those calculated for oceanic waters offshore illustrated in Fig. 3.1 likely reflects the signature of nearshore benthic metabolic processes rather than evidence of acidification over this ~10 year period.

Table 3.6. Significance of Mann-Whitney *U*-tests comparing carbonate parameters measured in surface waters with those at ~15 m depth for all data and by season.

	TCO$_2$	TA	pH	pCO$_2$	Ω_{arag}
Pooled data	< 0.0001	< 0.0001	< 0.01	< 0.001	< 0.001
Wet Season	< 0.001	< 0.001	< 0.01	< 0.01	< 0.01
Dry Season	< 0.0001	< 0.0001	ns	< 0.05	< 0.05

Millero *et al.* (1998) reported salinity normalized mean TCO_2 and TA values of 2045 μmol kg^{-1} and 2305 μeq l^{-1}, respectively for surface waters around the Galápagos Islands. In this study, $nTCO_2$ = 2087 μmol kg^{-1}, whereas nTA = 2295 μeq l^{-1}. The depletion of alkalinity in nearshore, coastal waters of the Galápagos reported herein is likely due to calcification in benthic communities, whereas the elevation in TCO_2 may reflect a community-wide dominance of respiration/calcification relative to photosynthesis. In other words, this increased CO_2 nearshore could reflect a dominance of heterotrophy over autotrophy in benthic communities (*i.e.*, community-wide respiration > photosynthesis).

In the Gulf of Panamá, pCO_2 values approach equilibrium with atmospheric pCO_2 during the nonupwelling wet season (Table 3.1). Regardless, the Ω_{arag} was

significantly depressed in the Gulf of Panamá relative to the Gulf of Chiriquí year-round (Table 3.2). Mean pCO_2 values in the Gulf of Chiriquí (Uva Reef) were slightly higher than atmospheric values. It is hypothesized that this is caused by shoaling of sub-thermocline waters with elevated CO_2. These results, although modest, show that the changes in carbonate chemistry induced by upwelling in Pacific Panamá primarily occur via the pulsed delivery of sub-thermocline waters high in TCO_2. This high TCO_2 is presumably a result of sub-thermocline waters accumulating CO_2 as a result of the microbial oxidation of organic matter below the mixed layer. This accumulated CO_2 is then vented to the atmosphere when these waters reach the surface.
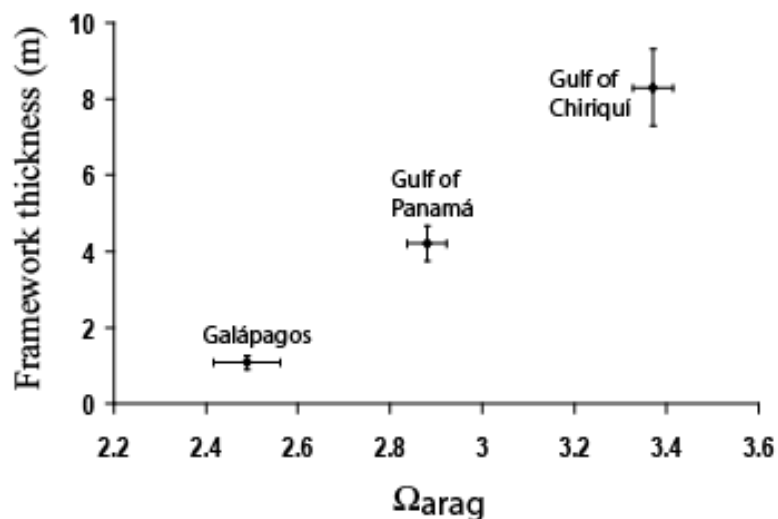
Figure 3.5. Ω_{arag} for eastern tropical Pacific reef sites plotted against framework thickness. Data points represent means ± SEM (standard error of the mean). Mean maximum framework thickness is greatest in the Gulf of Chiriquí (~8.3 m), intermediate in the Gulf of Panamá (~4.2 m), and least in the Galápagos (~1 m) (Glynn and Macintyre, 1977; Glynn and Wellington, 1983). Framework thickness for Galápagos was determined by taking the average maximum thickness of all pocilloporid reef sites as reported by Glynn and Wellington (1983) prior to the 1982-83 El Niño-Southern Oscillation (ENSO).

The carbonate chemistry at the Uva Reef was highly variable in both time and space. It was hypothesized that increased shoaling of the shallow thermocline within the dry season would act to raise TCO_2 and pCO_2 while lowering pH and Ω_{arag} (Fig.

3.2A). Indeed, pCO_2 values were higher and pH values lower during the dry season (Table 3.2). However, Ω_{arag} values were unexpectedly lower in the wet season when all data were examined. This was due to a higher nighttime TCO_2 during the wet season (Table 3.3). The greater relative enrichment of TCO_2 at night in the wet season (+ 53 μmol kg^{-1}) compared to the dry season (+ 27 μmol kg^{-1}) could be due to some unknown event and/or artifact of the temporal and spatial limitation inherent in trying to understand seawater CO_2 dynamics with discrete samples. The data presented in Table 3.1 only compare data collected during the day and the hypothesis of increased shoaling as a source of CO_2 can be accepted.

The significantly higher TCO_2 at depth on the Uva Reef, regardless of season, provides evidence that thermocline shoaling in the Gulf of Chiriquí is a source of CO_2 to the surface layers. Dana (1975) suggested that the cooler temperatures and increased turbidity associated with this shoaling acted to restrict reef growth to very shallow depths in the Gulf of Chiriquí (*i.e.*, < 10 m). This study shows that these sub-thermocline waters are enriched in CO_2 as well, which acts to significantly depress Ω_{arag}. This study does not attempt to reconcile which one of these variables is most important to reef development *per se*. Rather, it should be appreciated that the unique and dynamic physical forcing of the ETP results in an exceptionally narrow vertical window (< 10 m) over which reef growth is possible.

It will be interesting to track the carbonate chemistry of these areas as acidification progresses. Upwelling may act as a buffer when atmospheric pCO_2 eventually eclipses and surpasses the pCO_2 of these water masses. This atmospheric pCO_2 eclipse will occur first in Panamá (where surface pCO_2 does not exceed 500 μatm) and later in the Galápagos. The ability of the ETP to act as a natural laboratory for interdisciplinary research is therefore not limited to this study.

Chapter 4: Bulk skeletal density of reef-building corals and coral reef framework components from the eastern tropical Pacific

Density and Acidification

It has been hypothesized that lowered saturation states due to ocean acidification may cause reductions in coral skeletal density (Kleypas *et al*., 1999). Depressed skeletal density was suggested by measurements showing that the maximum compressive and bending strength of *Porites lobata* skeletons from the Pacific coast of Costa Rica are the lowest ever measured for scleractinian corals and are half that of Caribbean corals (Scott and Risk, 1988). This could be an artifact of the highly porous skeleton of corals in the family Poritidae; however, *P. lobata* samples with comparable porosities to the Caribbean coral *Acropora palmata* were still considerably weaker (Scott and Risk, 1988), which suggests that the *P. lobata* samples were indeed less dense. Depressed skeletal density has been noted in other calcareous organisms in the ETP as O'Dea *et al.* (2004) found that bryozoans in Pacific Panamá were lightly calcified relative to those from the Caribbean.

Bulk density and linear extension were assessed for five species of reef-building coral from the Uva Reef in Pacific Panamá. These measurements were done to establish baseline calcification rates given the following relationship:

Calcification (g CaCO$_3$ cm^{-2} yr^{-1}) = Extension (cm yr^{-1}) * Density (g CaCO$_3$ cm^{-3})

Additionally, bulk density measurements were made on previously collected specimens of *Porites lobata* from the Galápagos Islands and compared to those from the Uva Reef. The carbonate chemistry influencing the Uva Reef is much more favorable for coral calcification ($\Omega_{arag} > 3.3$) compared to that in the Galápagos ($\Omega_{arag} < 2.5$). The impetus was thus to determine if density varied significantly across a

geographic saturation state gradient. Density measurements of framework components collected in the Galápagos and Panamá were also compared.

Methods

Linear extension was measured *in situ* (Alizarin staining technique, Lamberts, 1978) on the Uva Reef (2003-04). After one year *in situ*, stained corals were collected and all tissue, epibionts, and infaunal organisms were removed via bleaching in non-aerated buckets. Corals with a massive morphology were then sliced using a diamond blade rotary saw, extension was measured with a hand-held ruler and values were rounded to the nearest millimeter. The skeleton of the two species of branching coral (*Pocillopora damicornis* and *P. elegans*) was translucent enough that extension could be measured without sawing. This was effective for determining the maximum linear extension per colony, but not useful when individual branch tips were measured for density and extension.

Coral collections archived in the Glynn lab were only used if clearly labeled. This yielded a small collection of *Porites lobata* colonies from the Galápagos (*n* = 5, collected in 1992 from Pta. Espejo, Marchena Is.) and Uva Reef (*n* = 6, collected in 1992). The *P. lobata* colonies from Galápagos correspond to those discussed in Glynn (1994) and were collected March 30, 1992. *P. lobata* colonies from the Uva Reef were collected February 16-21, 1992.

Subsamples for density determination were excised from the larger colonies. The methodology used for bulk density determination follows Archimedes principle and was compiled from Risk and Sammarco (1991), Bucher *et al*. (1998) and Smith *et al*. (2007). For coral species with a massive morphology, subsamples were taken from below the alizarin stain line (see Smith *et al*. 2007) and any areas of infaunal bioerosion were avoided (*e.g.*, *Lithophaga* spp. boreholes). Conversely, for

Pocillopora spp., subsamples were excised proximal, but above the stain line to represent new growth since staining. The idea here was to assess the amount of new $CaCO_3$ produced on a branch-by-branch basis for each pocilloporid colony. This was considered a highly conservative estimate of the amount of new $CaCO_3$ produced per unit area over a given time interval. All subsamples were soaked in a solution of sodium hypochlorite for at least 24 hrs or until all organic material was removed. Samples were then baked for at least 24 hrs at ~60 ^{o}C following which a dry weight was taken (DW_{clean}). Corals were then dipped in a bath of molten paraffin wax maintained at a temperature of ~110-115 ^{o}C (*sensu* Smith *et al.*, 2007). Once the samples cooled, a dry weight with wax was obtained (DW_{wax}), immediately followed by the measurement of a buoyant weight (BW_{wax}). Buoyant weight refers to the weight of an object when suspended in H_2O at 20 ^{o}C. Bulk density was then determined by the equations below:

$$Bulk\ Density = DW_{clean} / V_{enclosed}$$

$$V_{enclosed} = [DW_{wax} - BW_{wax}] \times [1.00\ g\ cm^{-3}]$$

Risk and Sammarco (1991) provided individual density measurements of *P. lobata* skeletons from the Great Barrier Reef (GBR) that were used for statistical comparisons with the corals in this study. Lough and Barnes (2000) also provide extensive density data on *P. lobata* skeletons from the GBR. The density values they report were determined using X-Ray densitometry and were not directly comparable to the density values reported by Risk and Sammarco (1991) and in this study.

Results

Inter- and Intraspecific variability in live coral skeletal density, extension, and calcification at the Uva Reef

Bulk skeletal density, linear extension, and calcification varied significantly between species of coral (Kruskal-Wallis tests, $p < 0.0001$ for density, extension and calcification) (Fig. 4.1, Tables 4.1 and 4.2). Density, extension, and calcification were greatest in the pocilloporidae. Values of density, extension, and calcification for the two pavonid species were less than the two *Pocillopora* species, but greater than *Porites lobata* (Fig. 4.1, Tables 4.1 and 4.2). Branches of *Pocillopora damicornis* ($n = 76$) were significantly more dense than those of *P. elegans* ($n = 66$; Mann-Whitney *U*-test, $p < 0.0001$). Mean extension was slightly higher in *P. damicornis* (2.82 cm yr^{-1}) compared to *P. elegans* (2.81 cm yr^{-1}), but these differences were not significant (Mann-Whitney, *U*-test, $p \gg 0.1$). Calcification (the product of density and extension) was significantly greater in *P. damicornis* compared to *P. elegans* (Mann Whitney *U*-test, $p < 0.001$).

Table 4.1. Bulk skeletal density and linear extension for five species of reef-building coral from the Uva Reef, Gulf of Chiriquí, Panamá. Mean, minimum and maximum values of coral colonies and subsamples reported if applicable.

Species	N	Density (g CaCO$_3$ cm^{-3})			Linear extension (cm yr^{-1})		
		Mean (± sem)	Min	Max	Mean (± sem)	Min	Max
Pocillopora	5 colonies	2.05 (0.022)	1.92	2.17	2.82 (0.11)	2.4	3.1
damicornis	76 branches	2.06 (0.014)	1.82	2.28	2.85 (0.057)	1.8	4.0
Pocillopora	8 colonies	1.89 (0.032)	1.82	2.02	2.81 (0.13)	2.5	3.1
elegans	66 branches	1.88 (0.011)	1.71	2.08	2.79 (0.05)	1.1	3.5
Pavona	6 colonies	1.67 (0.057)	1.44	1.85	1.21 (0.15)	0.7	1.7
clavus	34 subsamples	1.65 (0.031)	1.36	2.09	n/a	n/a	n/a
Pavona	5 colonies	1.56 (0.033)	1.31	1.87	1.12 (0.08)	0.9	1.3
gigantea	35 subsamples	1.55 (0.041)	1.23	2.23	n/a	n/a	n/a
Porites	6 colonies	1.39 (0.02)	1.21	1.48	0.80 (0.073)*	0.6*	1.0*
lobata	22 subsamples	1.39 (0.023)	1.13	1.55	n/a	n/a	n/a

*P. lobata usually died within the first 6 months of alizarin staining as inferred by the amount of new skeleton produced above the stain line. Extension rates thus represent a doubling of maximum 6 month extension and may underestimate *in situ* rates.
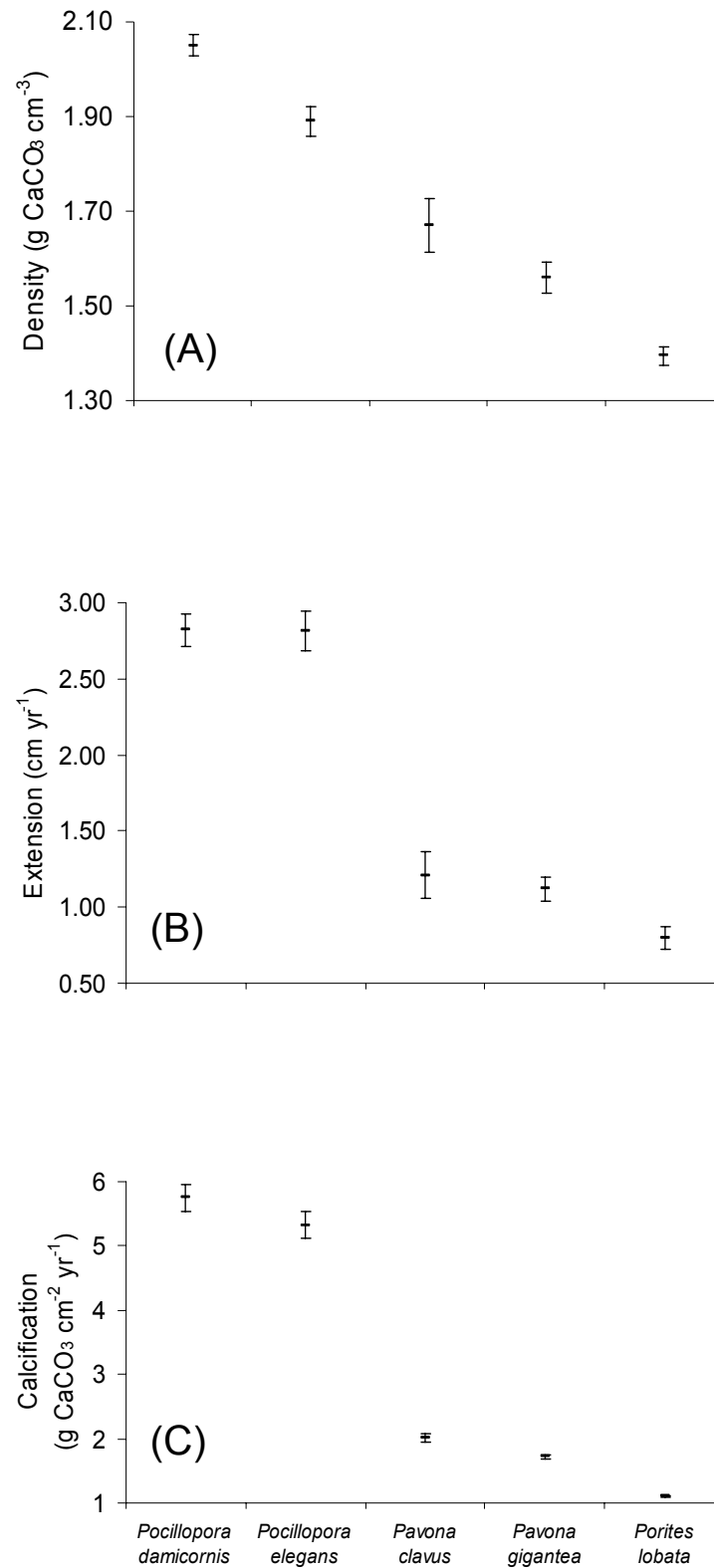
Figure 4.1. (A) Bulk skeletal density, (B) linear extension, and (C) calcification for five species of reef-building coral from Uva Reef, Gulf of Chiriquí, Panamá.

Density was inversely related to extension for all species of coral studied (Fig. 4.2). However, this relationship was only significant for three of the five species: *Pavona gigantea* ($r^2 = 0.43$, $n = 35$, $p < 0.0001$), *P. clavus* ($r^2 = 0.16$, $n = 34$, $p = 0.02$), and *P. damicornis* ($r^2 = 0.13$, $n = 76$, $p = 0.0013$). Figure 4.3 illustrates the scatter in skeletal density measured over a range of values for linear extension when both species of *Pocillopora* are pooled.

Table 4.2. Ranges of calcification rates determined from multiplying mean, minimum and maximum bulk density values by linear extension. Large range in values is indicative of large degree of multiplicative error inherent in this method.

Species	N	Calcification (g $CaCO_3$ cm^{-2} yr^{-1})		
		Mean (± sem)	Min	Max
Pocillopora damicornis	5 colonies	5.75 (0.21)	5.27	6.65
	76 branches	5.86 (0.109)	3.90	8.17
Pocillopora elegans	8 colonies	5.32 (0.21)	4.61	6.27
	66 branches	5.24 (0.092)	1.88	6.45
Pavona clavus	6 colonies	2.01 (0.063)	1.15	2.69
	34 subsamples	2.10 (0.093)	1.05	3.02
Pavona gigantea	5 colonies	1.72 (0.037)	1.49	2.06
	35 subsamples	1.76 (0.036)	1.44	2.45
Porites lobata	6 colonies	1.10 (0.019)	0.85	1.44
	22 subsamples	1.12 (0.053)	0.76	1.55

Table 4.3 shows the mean, minimum and maximum bulk skeletal density measured in colonies of *Porites lobata* collected from the Galápagos and Panamá in 1992. *P. lobata* from Galápagos were significantly less dense than those from the Uva Reef in Panamá (Mann-Whitney *U*-test, $p < 0.01$). If we pool the density data from Galápagos and Panamá into an ETP category, we find that *P. lobata* skeletons from the GBR ($n = 27$) were significantly more dense than those from the ETP ($n = 93$, *t*-test assuming equal variances, $p < 0.05$, Table 4.4). This difference was mainly a result of the low density Galápagos samples, as the Panamá samples by themselves ($n = 48$) were no different than those from the GBR (Mann-Whitney *U*-test, $p > 0.1$) (Fig. 4.4).
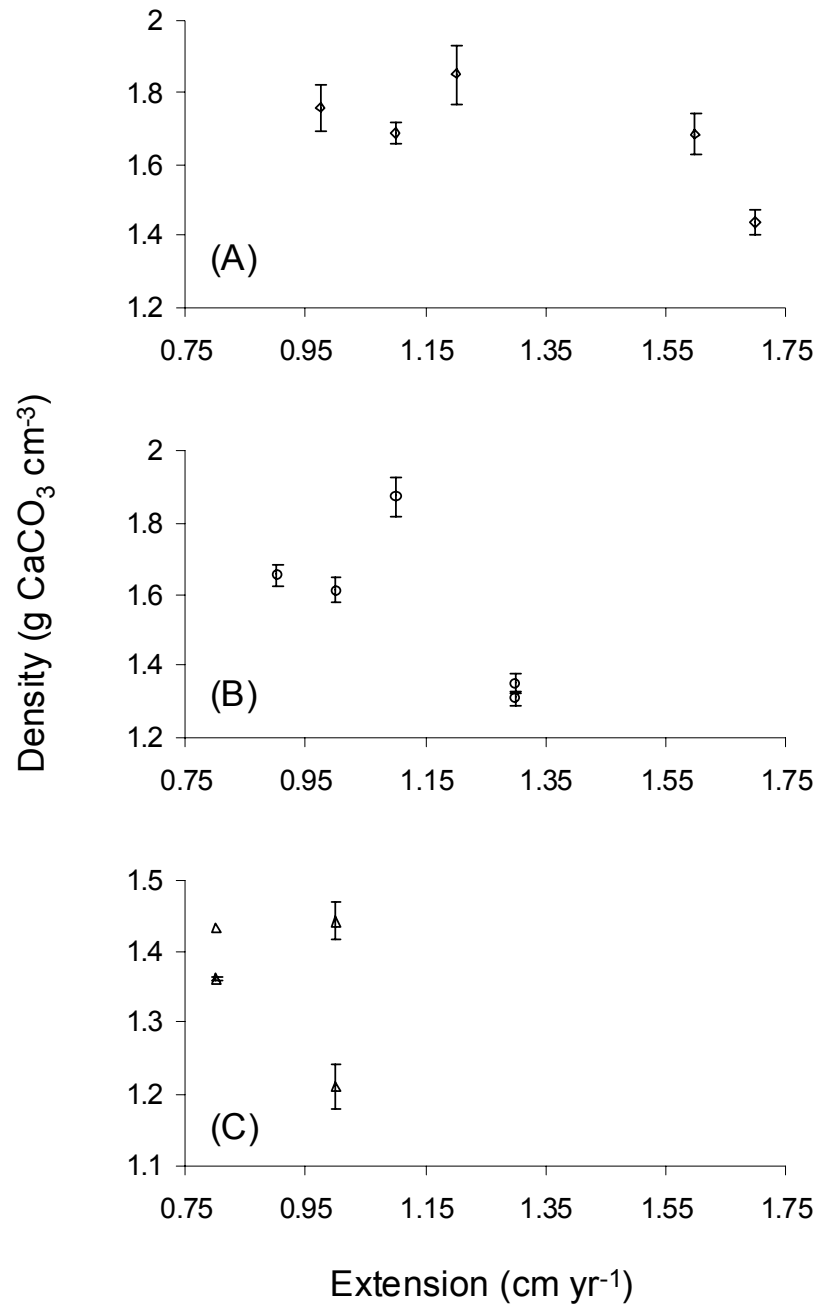
Figure 4.2. Relationship between linear extension and bulk skeletal density for corals from Uva Reef, Gulf of Chiriquí, Panamá with massive morphology: (A) *Pavona clavus*, (B) *Pavona gigantea*, and (C) *Porites lobata*. Each point represents a mean value for an individual colony. Error bars represent the standard error of the mean for density measurements. Note that there are no error bars for extension as one extension value (*i.e.*, maximum) is used per colony for species with a massive morphology. *P. lobata* colonies grew for approximately 6 months after staining and then died. Extension rates were estimated as twice the measured six month extension value (*i.e.*, 0.3 – 0.5 cm).

Table 4.3. Bulk skeletal density of *Porites lobata* colonies from Galápagos and Panamá (Uva Reef, Gulf of Chiriquí)

Site	Sample No.	# Subsamples	Density (g $CaCO_3$ cm^{-3})		
			Mean (± sem)	Min	Max
Galápagos	1	8	1.22 (0.033)	1.03	1.34
	2	9	1.30 (0.025)	1.20	1.46
	3	8	1.20 (0.043)	1.04	1.43
	4	12	1.11 (0.044)	1.04	1.19
	5	8	1.34 (0.044)	1.22	1.56
			Avg. = 1.23		
Panamá	1	7	1.39 (0.018)	1.32	1.46
	2	8	1.37 (0.030)	1.23	1.46
	3	11	1.23 (0.018)	1.13	1.36
	4	14	1.21 (0.018)	1.13	1.35
	5	6	1.43 (0.014)	1.40	1.49
	6	2	1.39 (0.018)	1.37	1.41
			Avg. = 1.34		

Table 4.5 summarizes linear extension values reported for *Pocillopora damicornis* in the primary literature across the Pacific Ocean compared to those values measured in Panamá. Statistical comparisons were not possible given the lack of data reported in these prior studies.
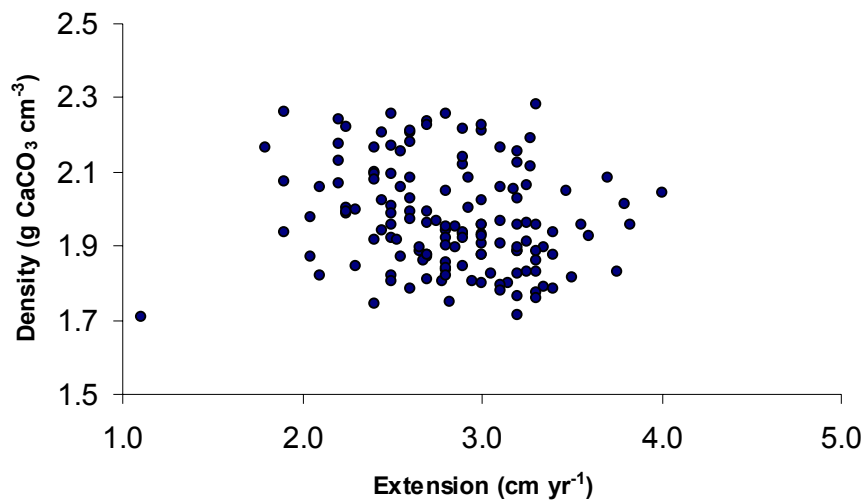
Figure 4.3. Relationship between linear extension and bulk skeletal density for branches of *Pocillopora* spp. from Uva Reef, Gulf of Chiriquí, Panamá.
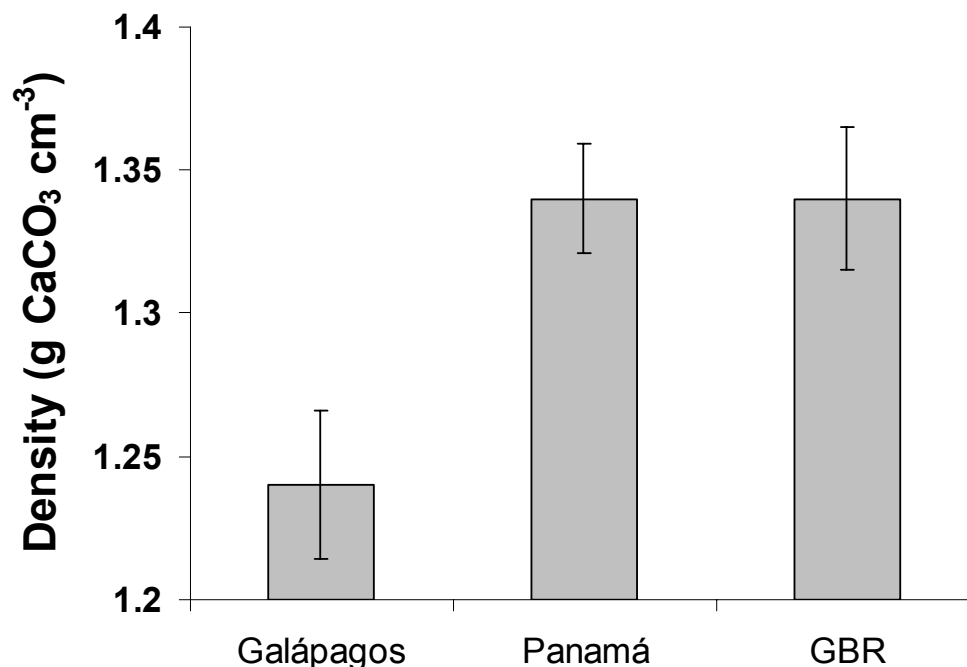
Figure 4.4. Bulk skeletal density of *Porites lobata* from Galápagos, Panamá, and the Great Barrier Reef (GBR), Australia. Data points represent means (± standard error of the mean) and values for the GBR taken from Risk and Sammarco (1991), whereas values for Galápagos and Panamá are presented in this study.

Table 4.4. Average skeletal density, extension rate, and calcification rate for *Porites lobata* colonies from Panamá and Galápagos compared to values reported in primary literature. Minimum and maximum values are in parenthesis if available.

Location	Density	Extension	Calcification	Reference
Galápagos	1.23 (1.03 – 1.56)	0.89 (0.5-1.4)	1.09 (0.52-2.18)	Density: This study Extension: Glynn, 1994
Panamá (Uva Reef)	1.34 (1.13 – 1.49)	0.81 (0.6 – 1.0)	1.12 (0.76 – 1.55)	This study
Samoa*	1.47 (1.41-1.53)	0.45 (0.12-0.98)	0.65 (0.19-1.39)	Smith *et al.*, 2007
GBR[†]	1.28 (0.92-1.96)	1.29 (0.53-2.27)	1.63 (0.6-2.85)	Lough and Barnes, 2000
GBR[†§]	1.29 (1.25 – 1.32)	1.40 (1.28-1.52)	1.78 (1.59-1.96)	Cooper *et al.*, 2008
GBR	1.34 (1.05 – 1.59)	?	?	Risk and Sammarco, 1991
Hawai'i[†‡]	1.35 (1.15 – 1.7)	1.25 (1.0-1.5)	1.69 (1.15-2.55)	Grigg, 1982

*-Average of all group means reported by Smith *et al.*, 2007. Note that calcification rates reported are upward, not lateral and values in parentheses represent min. and max. means, not individual measurements

[†]-The density values reported in this study were obtained through X-Ray densitometry rather than Archimedes principle, thus the values may not be directly comparable to other studies presented.

[‡]-Note that values for Hawai'i are estimates based on data points plotted in Fig. 3A of Grigg (1982).

[§]-The ranges of values reported for this study represent average values for the years 1988 and 2003. Maximum values occurred in 1988, whereas minimum values were measured in 2003. These authors attribute this decline to the combined effects of warming and acidification over this period.

Table 4.5. Comparison of linear extension measured in *Pocillopora damicornis* across the Pacific Ocean. Extension values for *P. elegans* from Panamá included for comparison.

Species	Location	Extension		Reference
		Mean maximum branch length per colony	Mean of all branches per colony	
Pocillopora damicornis	Uva Reef, Panamá	3.7	2.82	This study
Pocillopora damicornis	Secas Is. Panamá	3.9	3.2*	Glynn, 1977
Pocillopora damicornis	Uva Reef Panamá	3.6	?	Eakin, 1996
Pocillopora damicornis	Saboga Reef, Panamá	2.4	?	Glynn and Stewart, 1973
Pocillopora damicornis	Samoa	?	2.5*	Mayer, 1924
Pocillopora damicornis	Hawaii	?	0.98*	Edmondson, 1929
Pocillopora elegans	Uva Reef, Panamá	3.4	2.81	This study

*-Represents median values of pocilloporid growth for Panamá, Samoa (Mayer, 1924) and Hawai'i (Edmondson, 1929) as reported by Glynn (1977).

Bulk density of framework components in Panamá and Galápagos

Bulk density of framework components varied significantly with substrate of origin in Panamá and Galápagos (Krusal-Wallis tests, $p < 0.0001$ in both regions). Framework components derived from *Pocillopora* spp. were the densest substrate measured in Panamá, followed in order of decreasing density by *Pocillopora* pieces heavily encrusted with crustose coralline algae (CCA), and CCA (Table 4.6). Density values for *Pocillopora* framework components were no different between reef sites located within the Gulf of Chiriquí in Panamá (*t*-test assuming unequal variances, $p > 0.1$) (Table 4.6) and these values, when pooled for Panama ($n = 121$) were no different than Galápagos ($n = 83$, *t*-test assuming equal variances, $p > 0.1$). CCA framework components were significantly denser from the Uva Reef compared to the

Dog Island Reef, both of which are located in the Gulf of Chiriquí, Panamá (Mann-Whitney *U*-test, *p* < 0.01). However, this may reflect the small sample sizes rather than any real significance (Table 4.6). Framework components heavily encrusted with CCA were not observed in Galápagos. Encrustation by CCA in Panamá coincided with a depressed bulk density of framework material (Table 4.5). Dead *Pocillopora* framework components from Panamá were significantly less dense than their living source material (Mann-Whitney *U*-test, *p* < 0.0001).

Table 4.6. Density variability in framework components with differing origins from Galápagos and reef sites in the Gulf of Chiriquí, Panamá.   The vast majority of framework encountered was derived from *Pocillopora* spp. Encrustation by CCA was prolific in Panamá, but nearly non-existent in Galápagos.

Site	Substrate type	*n*	Density (g CaCO$_3$ cm^{-3})		
			Mean (± sem)	Min	Max
Galápagos	*Pavona* sp.	6	1.62 (0.118)	1.25	1.89
	Pocillopora spp.	83	1.71 (0.022)	1.11	2.22
	Porites lobata	10	1.22 (0.026)	1.12	1.37
	Psammacora	8	1.81 (0.015)	1.70	1.86
Panamá Gulf of Chiriquí Uva Reef	*Pocillopora* spp.	84	1.66 (0.024)	1.22	2.16
	Pocillopora heavily encrusted with CCA	52	1.58 (0.015)	1.35	1.78
	CCA	7	1.54 (0.079)	1.33	1.99
Secas Is. Dog I. Reef	*Pocillopora* spp.	37	1.69 (0.026)	1.36	2.02
	Pocillopora heavily encrusted with CCA	1	1.54	-	-
	CCA	5	1.32 (0.022)	1.28	1.40

Discussion

This study establishes baseline calcification rates for five species of reef-building coral from the Uva Reef in Pacific Panamá that will be important endpoints by which to assess future change. These results represent inexpensive, standardized methods that will be easy to repeat efficiently. Although extension may be correlated

to calcification, this relationship is not perfect and varies as there is evidence that some corals can maintain extension rates in marginal environments through "stretch-modulation" (Edinger *et al.*, 2000; Carricart-Ganivet and Merino, 2001; Cook *et al.*, 2002; Cruz-Piñon *et al.*, 2003), which allows them to maintain linear growth at the expense of skeletal density. Thus, the endpoint that needs to be monitored is calcification, not extension, as the latter may be misleading. For instance, note the large range in 'average' linear extension reported for *Pocillopora damicornis* across the Pacific Ocean (Table 4.5). This table illustrates the difficulty associated with making comparisons based on extension alone, albeit the data reported for the other Pacific sites does fall within the range reported for Panamá documented in multiple studies over 30 years (e.g., Glynn and Stewart, 1973 and the studies that follow listed in Table 4.5). The high calcification rates documented for both species of *Pocillopora* may explain why these two species are the most important reef builders of the ETP (Glynn and Maté, 1997, Cortés, 1997). The relatively high skeletal densities likely increase the preservation potential for these species.

Wellington and Glynn (1983) reported a mean density of 1.86 g cm^{-3} and annual extension rate of 0.93 cm yr^{-1} for *Pavona clavus* colonies in the Gulf of Chiriquí. This translates to a mean annual calcification rate of 1.73 g cm^{-2} yr^{-1}, which is lower than the mean presented herein, but still falls within the range of values (Table 4.2). Mean density of *P. clavus* in the present study was less than that reported by Wellington and Glynn (1983), albeit extension was greater. This resulted in comparable calcification rates between these two studies, which may illustrate the phenomenon of "stretch-modulation" described by Carricart-Ganivet and Merino (2001). In other words, although extension and density may vary significantly across physical habitat gradients, calcification rate remains relatively conservative. Indeed,

Scoffin *et al*. (1992) showed that calcification in *Porites lutea* was relatively constant over 11 separate reefs with differing exposure to wave energy and turbidity. Instead, they showed that bulk density was the most sensitive growth parameter and increased along a gradient of increasing hydrodynamic energy, whereas extension decreased. These results are among the best existing evidence supporting the hypothesis of 'stretch-modulation' in coral growth.

It is intriguing that Wellington and Glynn (1983) found that low density band (LD) formation in both species of *Pavona* occurred during the dry season in both the Gulf of Chiriquí and Gulf of Panamá. Increased thermocline shoaling and upwelling in the Gulf of Chiriquí and Gulf of Panamá, respectively, coincides with the timing of LD band formation. These authors show that the start of LD band formation in the Gulf of Panamá was initiated two weeks after the start of upwelling and ceased six weeks post-upwelling. A ~50% reduction in community-wide calcification occurred as a result of nutrient enrichment (both N + P) at One Tree Island on the Great Barrier Reef, and this effect persisted for one month following the cessation of nutrient enrichment (Kinsey and Davies, 1979). These workers hypothesized that this persisting effect was due to the crystal poison effect of phosphate (Simkiss, 1964). The similarity in the time it takes for HD band formation to resume in Panamanian corals post-upwelling (*i.e.*, six weeks) is suggestive of a lasting inhibitory effect of elevated phosphate concentrations during upwelling. Indeed, Ferrier-Pages *et al*. (2002), found no recovery in calcification rates for corals exposed to elevated P concentrations. They did observe recovery in calcification for corals after exposure to N-enrichment or N and P combined. They hypothesize that P may have long-lasting effects on skeletal formation (and even be retained in the skeletal matrix), whereas N and N+P are incorporated into increased algal biomass, which decreases when

nutrient enrichment is stopped. Thus, LD band formation in massive corals from Panamá may be due to a fertilization effect on zooxanthellae populations within coral tissues. High density (HD) band formation occurs in the wet season when upwelling processes across both gulfs are 'shut off' and nutrient concentrations in the surface layers are similarly low (D'Croz and O'Dea, 2007). HD formation coincides with increased gamete production, thus the negative effects of upwelling may not be limited to calcification. Future studies should attempt to reconcile the combined effects of lowered saturation state and elevated nutrient concentrations on coral calcification. The sole study that has been done found that elevated nutrient concentrations acted to ameliorate the effects of elevated pCO_2 (Langdon and Atkinson, 2005). Clearly, a lot remains to be learned regarding the process of coral calcification and its relationship to ambient environmental variability. A better understanding of these relationships will help us better understand and predict the effects of acidification upon biologically-mediated calcification. Incorporation of ambient carbonate chemistry and nutrient data (at relevant spatial and temporal scales) into studies of coral skeletogenesis may resolve some of mystery associated with density band formation in massive corals.

The calcification rates presented for *Porites lobata* are consistent with those previously published (Table 4.4). However, evidence is provided that *Porites lobata* skeletons are significantly less dense in the Galápagos relative to those collected from the Uva Reef in Panamá (Table 4.3). Indeed, the values documented in this study fall on the low end of values previously published, suggesting a regional depression of skeletal density (Table 4.4). Density measurements of *P. lobata* colonies from the Uva Reef were no different than those from the GBR, however, the Galápagos

samples were significantly less dense than both these sites. It is hypothesized that these differences are due to regional differences in the saturation state of aragonite.

The post-mortality loss of density that occurs in *Pocillopora* may be due in part to the activities of infaunal bioeroding organisms (compare density values of living and dead *Pocillopora*, Table's 4.1 and 4.6). Although not quantified, the abundance of boring Clionid sponges was observed to be particularly high within the intraseptal spaces of *Pocillopora* framework components. The sponges appeared to most often grow parallel with the growth axis of the *Pocillopora* skeleton (Fig. 4.5). This growth strategy is hypothesized to follow the path of least resistance within the pocilloporid skeleton. It likely is much less costly for sponges to bore through individual dissepiments and grow along the growth axis rather than attempt to breach the dense outer wall. Sponges were also observed within the intraseptal spaces of pocilloporid framework components from the Galápagos. The activity of these sponges may also partially explain why there were no significant differences in the density of pocilloporid framework components across the ETP (Table 4.6). However, this is merely speculation at this point without comparable skeletal density data for living pocilloporid corals from the Galápagos. Furthermore, abiotic dissolution of framework components cannot be ruled out.

This study provides empirical evidence that the regionally depressed saturation state in the equatorial eastern Pacific may be causing corals to secrete a less dense skeleton. Density values of corals collected from the Uva Reef in Pacific Panamá were lower, but not significantly different from those collected on the GBR. Carbonate saturation state values measured on the Uva Reef were the highest documented throughout the ETP during this study (Chapter 3). Conversely, those corals from the Galápagos, which had the lowest carbonate saturation state

documented in this study, were significantly less dense relative to those from Panamá and the GBR. It is interesting that the density of non-living pocilloporid framework components were no different across the ETP saturation gradients. This could be a result of the activity of boring sponges removing the primary carbonate material within the dead coral skeleton, thus lowering density, albeit physico-chemical dissolution cannot be ruled out.
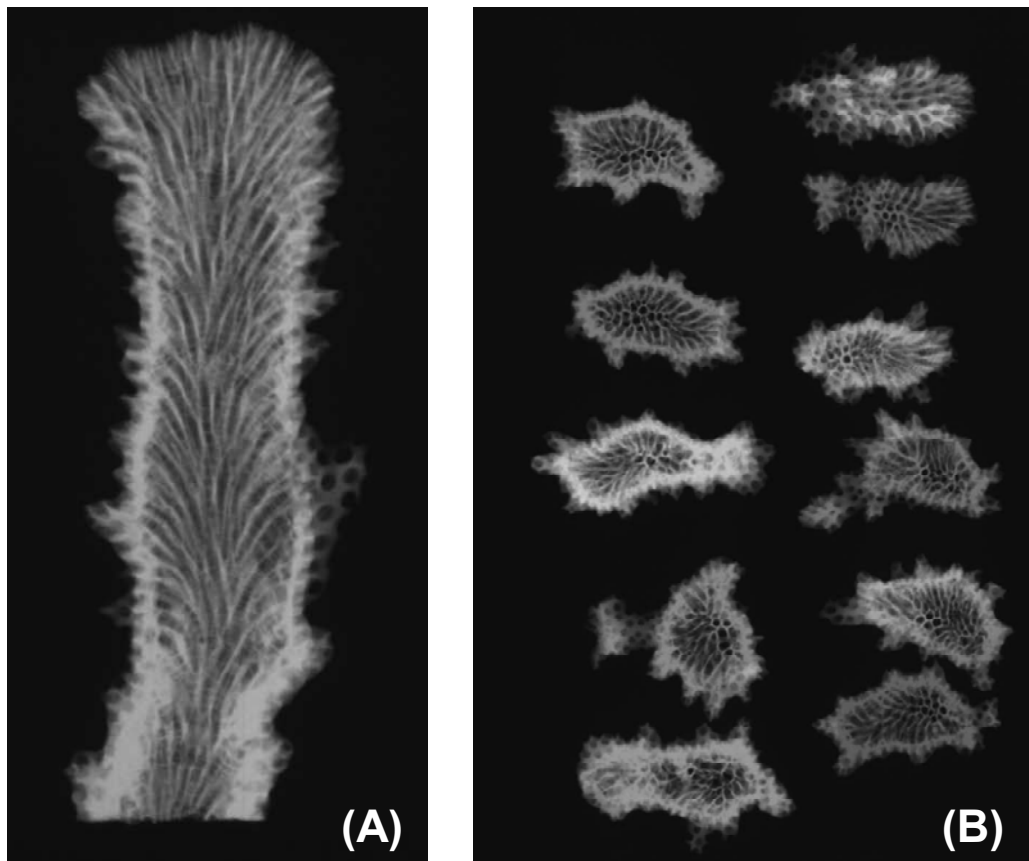
Figure 4.5. X-Ray of *Pocillopora* branch sliced (A) parallel to the growth axis and (B) perpendicular to the growth axis. Note how skeletal structure is much denser on periphery relative to interior. The diameter of individual branches is about 1 cm.

In a recent study, Cooper *et al*. (2008) suggest that declines in coral calcification observed on the GBR over the past 20 years may be a result of combined warming and acidification. These changes were mainly a result of declines in linear extension rather than a depression in density, although slight density declines were

observed. If we consider these results along side those presented herein, it seems that

acidification may cause reductions in both extension and density.

Chapter 5: Overall Conclusions

Synthesis

The increased frequency and severity in coral bleaching events observed world-wide in the past 25 years suggest that coral reefs are already being significantly impacted by warming. Each bleaching event on the Florida Reef Tract has progressively worsened since the initial descriptions of highly localized bleaching by Mayer (1914), Shinn (1966) and Jaap (1979). For instance, the last three bleaching events in Florida have all spanned the entire reef tract. The work presented here suggests that simple bleaching thresholds based on deviations above the climatological maximum monthly sea temperature are just as effective at identifying bleaching years as complex thermal stress indices (*e.g.*, time-integrated bleaching curves of Berkelmans, 2002a). Real-time bleaching alerts by NOAA's Integrated Coral Observing Network (ICON: see Hendee *et al.*, 2006) are now based upon a running 30-day average SST. Alerts are now issued only when the running 30-day average SST exceeds the estimated bleaching threshold for a particular site.

In addition to three widespread, mass-coral bleaching events, the Florida Reef Tract was impacted by three tropical storms and 12 hurricanes since 1997. It is well documented that physical impacts from storms can be devastating to coral reef ecosystems (Harmelin-Vivien, 1994), but the damage caused by storms is highly variable between and within affected reefs (Lirman and Fong, 1997). Severe damage to coral reefs has been observed and predicted to occur on reefs up to 30 to 90 km from a storm's center (Done, 1992; Woodley, 1992; Scoffin, 1993). Based on the spatial and temporal correlation between coral bleaching events and hurricanes, it has been hypothesized that bleached corals may benefit from cooling associated with

hurricane passage (Glynn, 1996). Chapter 2 documents the nearshore thermal response to tropical storm and hurricane passage on the Florida Reef Tract. These data have been used to show that the sea surface cooling that resulted from the high frequency of hurricanes that impacted Florida in 2005 likely acted to ameliorate the severity and duration of bleaching (Manzello *et al.*, 2007).

It appears that low Ω_{arag} is an additional factor in the poor reef development throughout the eastern tropical Pacific. The highest Ω_{arag} values documented in this study occur in the Gulf of Chiriquí, which corresponds with the greatest reef development and highest coral species diversity of the entire eastern Pacific (Glynn *et al.*, 1972; Dana, 1975; Glynn and Maté, 1997). Seasonal upwelling had a significant effect on the carbonate chemistry of surface waters in Panamá. During upwelling (dry season), salinity and TCO_2 values were significantly higher, but temperature and Ω_{arag} were significantly lower in the Gulf of Panamá compared to the Gulf of Chiriquí. TA, pH and pCO_2 were no different between gulfs in the dry season suggesting that the chemical signature of upwelled waters is similar across gulfs and the differences appear to reflect the greater intensity of upwelling in the Gulf of Panamá. During the nonupwelling wet season, salinity, TCO_2, TA, and Ω_{arag} were significantly depressed in the Gulf of Panamá relative to the Gulf of Chiriquí. However, pCO_2 and pH were no different between the Gulf of Panamá and Gulf of Chiriquí during this time (Table 3.2B) showing that wet season differences between Panamanian gulfs may reflect differential freshwater dilution of the surface layers. It will be interesting to track the carbonate chemistry of these areas as acidification progresses. Upwelling may act as a buffer when atmospheric pCO_2 eventually eclipses and surpasses the pCO_2 of these water masses. This atmospheric pCO_2 eclipse will occur first in Panamá (where surface pCO_2 does not exceed 500 µatm) and later in the Galápagos. The ability of

the ETP to act as a natural laboratory for interdisciplinary research is therefore not limited to this study.

The regionally depressed Ω_{arag} in the equatorial eastern Pacific appears to be resulting in corals with a less dense skeleton. Density values of corals collected from the Uva Reef in Pacific Panamá were lower, but not significantly different from those collected on the Great Barrier Reef (GBR). Conversely, those corals from the Galápagos, where Ω_{arag} was the lowest documented in this study, were significantly less dense relative to those from Panamá and the GBR. It is interesting that the density of non-living pocilloporid framework components were no different across the ETP saturation gradients. This could be a result of the activity of boring sponges removing the primary carbonate material within the dead coral skeleton, thus lowering density, albeit physical/chemical dissolution cannot be ruled out.

Implications

The increased severity and frequency of coral bleaching events over the past 100 years (*e.g.*, Glynn, 1993) is generally well-accepted as an indicator of anthropogenically-induced global warming (Hughes *et al.*, 2003). It has been suggested that bleaching events may be an annual occurrence on the GBR beginning around the year 2050 (Hoegh-Guldberg, 1999). The evidence presented in Chapter 1 shows that bleaching thresholds are 'set' by the climatological annual maximum monthly sea temperature and show no evidence of changing with repeated bleaching.

Hurricane cooling is not expected to nullify the proposed effects of climate change on coral reefs (e.g., Hoegh-Guldberg, 1999; Hughes *et al.*, 2003); however, instances in which hurricane and bleaching events co-occur can have a significant effect on coral reef persistence. The area of cooling extends substantially (~700 km) outside the narrow swath of physical damage (< 90 km) providing empirical evidence

that the passage of a hurricane can proportionally benefit a much greater area than it disturbs when corals are thermally stressed.

While warming may be clearly visible as large-scale, synchronized bleaching of entire reefs and reef regions, the effects of ocean acidification are likely to be subtle and remain unseen. Acidification is expected to reduce coral reef calcification and increase reef dissolution (Kleypas *et al*., 1999; Langdon *et al*., 2000; Yates and Halley, 2006). Eastern Pacific reef development appears strongly dependent upon Ω_{arag} (Fig. 3.5). This implies that reef development and accretion may be severely limited in a high CO_2 world.

Altogether, these results suggest that the high frequency and intensity of bleaching events as a result of warming will be the most deleterious impact of climate change on coral reef ecosystems over the next 100 years. This ongoing mass-mortality of reef corals will greatly reduce the production of $CaCO_3$ on coral reefs in the short-term regardless of acidification. It is hypothesized that the most serious threat posed by acidification to coral reefs will be the inability of reefs to recover from recurrent bleaching disturbances. This will be due to 1) reduced calcification rate in surviving coral tissues and new recruits because of depressed Ω_{arag} and 2) a reduced amount and/or stability of framework components. It is important to point out that acidification will cause a chronic reduction in calcification 24 hrs-a-day, 7 days-a-week, 365 days-a-year. To-date, disturbances associated with warming have been acute, but short-term.

Reef framework structures may already be in a "net erosional" state in areas where live coral cover is low (*i.e.*, Florida Reef Tract). Indeed, Eakin (1996, 2001) has shown that the Uva Reef in Pacific Panamá became net erosional following the 1982-83 ENSO-associated mass mortality of reef corals. Given that Uva Reef has

recently shown prolific signs of recovery in live coral cover (pers. obs.), future work should determine if this site has reverted back to an accretional state.

Unanswered questions, possible solutions and future research

While ETP reefs may provide insights into the future of coral reef development in a high CO_2 world, the observations are confounded by the coincidence of low Ω_{arag} with high nutrients and low temperatures (Fig. 5.1). High phosphate levels inhibit aragonite precipitation in natural seawater (see Morse *et al*., 2007 and refs. cited therein) and could also be a factor in the low density of Galápagos corals. However, the nutrient values presented in Fig. 5.1B are only coarsely resolved temporally and spatially, and a better understanding of the natural variation in nutrient concentrations on ETP reefs is required before we can interpret the potential limiting role of nutrients.
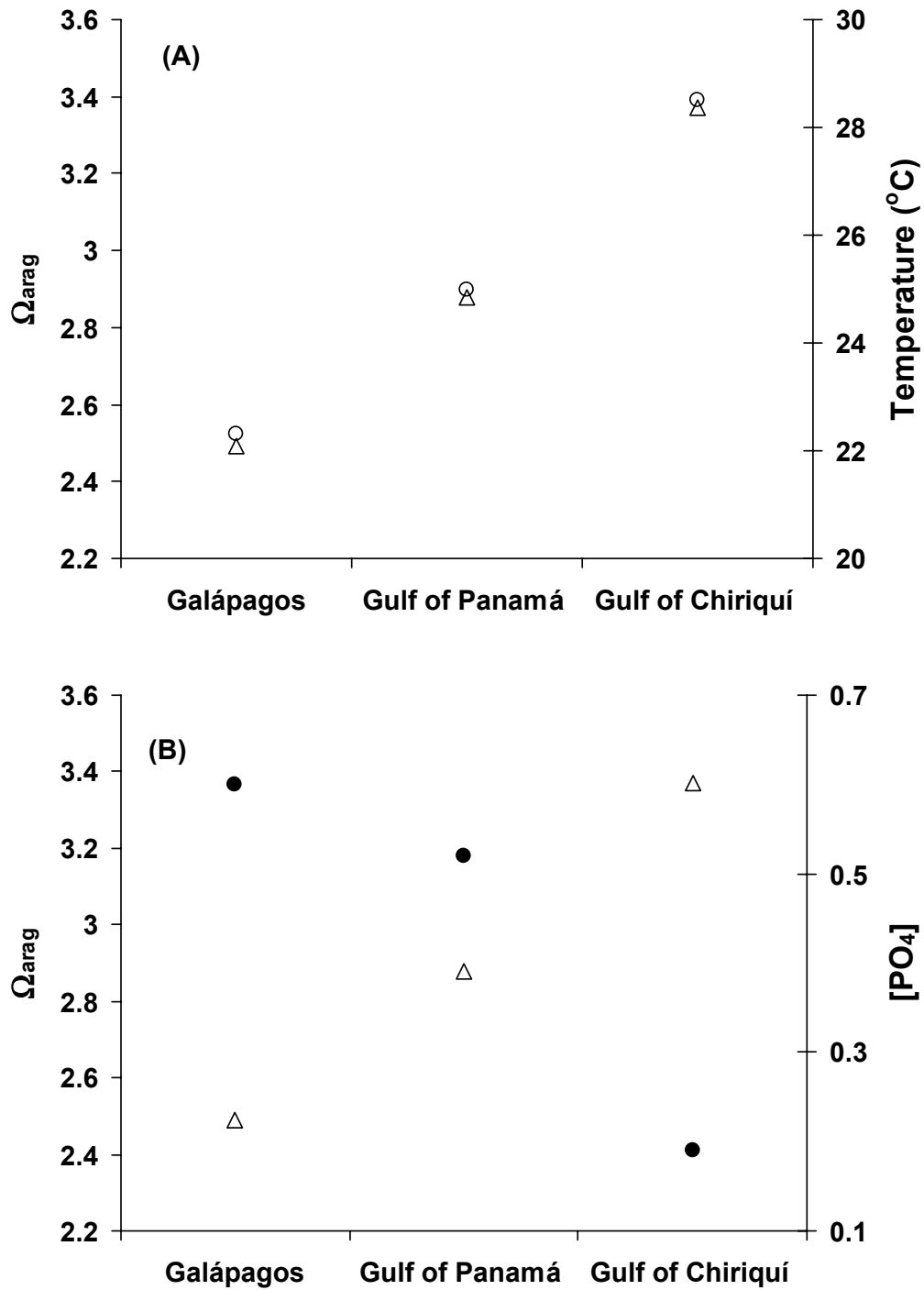
Figure 5.1. Relationship of Ω_{arag} (open triangles in both plots) with (A) temperature (open circles) and (B) phosphate concentration (closed circles). Note inverse relationship between Ω_{arag} and phosphate concentration. Values for phosphate identical to those reported in footnote to Table 3.1.

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