

*Millennial-scale record of Goniopora spp. coral growth rates from the inshore Great Barrier Reef reveals a long-term decline and recent recovery trajectory.*

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### *Statement of Authorship*

The research carried out in the course of this investigation and the results presented in this report are, except where acknowledged, the original work of the author, and all research was conducted during the Honours program.

### **Contributions by Others to the Thesis:**

*George Roff* collected sediment cores and provided U-series dates and data for the cores analyzed in this study.

*Simon Blomberg* provided guidance on statistical methods.

*Peter Colls* thick-sectioned coral fragments.

All other contributions are cited in-text.

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Examiners please note:

Honours marks are recorded on transcripts using the 1-7 marking system, which does not coincide with the class marking system. Most international universities will only use the transcript mark for admission into PhD programs, so please consider the appropriate transcript mark in addition to the class mark.

<i>Transcript Mark</i>	<i>Honours Class Mark</i>	<i>Percentage</i>
7	I	> 85%
6	I	80 - 84%
6	IIa	75 - 79%
5	IIa	70 - 74%
5	IIb	65 - 69%
4	IIb	60 - 64%

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### **Abstract**

Inshore reefs from the Great Barrier Reef were subject to an increase in the magnitude and frequency of sediment flux following European settlement (~1862). Characterizing the relationship between anthropogenic disturbance and metrics of coral stress has proven difficult, due in part to a lack of historical data. We examined a ~900-year record of coral growth from two inshore reefs (Pandora and Havannah) of the central Great Barrier Reef. We analyzed annual coral growth rates (linear extension) through time from colonies of a dominant genus of inshore coral (*Goniopora* spp.) We found a 38% decrease in *Goniopora* linear extension rates over the 900-year record, with a majority of the decline occurring after 1580. The decline in linear extension predated European settlement in the region, and is strongly predicted by sea surface temperature and river discharge. Surprisingly, *Goniopora* growth rates increased from 1980-2005, despite increasing intensity of anthropogenic influence on the adjacent Burdekin River catchment during this time. This increase in extension rate contrasts with previous studies of linear extension in *Porites* spp. from the inshore Great Barrier Reef. Despite a long-term decline in linear extension rates, reef accretion rates as determined from sediment cores were remarkably consistent, suggesting that coral growth rates are decoupled from reef accretion rates over centennial scales. This study highlights the variability in response of inshore corals to anthropogenic disturbance, and emphasizes the long-term effects of climate influence on coral growth rates.

## **Introduction**

Coral reefs throughout the world are declining in coral cover (Gardner *et al.* 2003; Bruno & Selig 2007), have reduced functionality and resilience (Nystrom *et al.* 2000), and individual coral colonies are suffering degraded health (Richardson 1998) wherever intensive human influence is present (Hughes *et al.* 2003). Global increases in temperature and atmospheric carbon dioxide threaten coral reefs and will have unknown interactions with local stressors in the future (Hoegh-Guldberg *et al.* 2007), yet it is clear that the rate of increase and the magnitude of pressure on reefs from anthropogenic disturbance is unprecedented in their history (Pandolfi *et al.* 2003). Though some stressors are well documented (see Hughes & Connell 1999) and there is a spatial co-occurrence of reef degradation and adjacent human development (Richmond 1993), establishing causality between coastal anthropogenic disturbance and the decline of coral reefs has proven difficult, due in part to a lack of temporal data (McCulloch *et al.* 2003; Fabricius 2005). Understanding baselines of natural variability on reefs in space and time is of critical importance to be able to differentiate between coral degradation caused by anthropogenic influence, and natural changes in coral reef systems.

Coral skeletons form the structural complexity of reefs that provides habitat for a tremendous diversity of life (Roberts & Ormond 1987), and actively accreting reefs require enough production of carbonate by corals and other calcifiers to exceed erosion and off-reef transport. Coral skeletons grow by precipitating calcium carbonate in the form of aragonite, and the rate, density and geochemical composition of the deposition varies according to environmental conditions (Wells 1963; Dodge & Vaisnys 1975). As light and temperature fluctuates seasonally, distinct and alternating high and low density bands are formed in some coral taxa (Knutson *et al.* 1972).

Coral skeletons are chronometers of growth and recorders of environmental conditions simultaneously, which is useful for reconstructing proxies of sea surface temperature (SST; Lough & Barnes 1997), pH (Pelejero *et al.* 2005), aragonite saturation (Pelejero *et al.* 2005), freshwater discharge (Isdale *et al.* 1998) and sedimentation (McCulloch *et al.* 2003). In addition to incorporating geochemical tracers into the skeleton during deposition, coral calcification rates can be affected by these environmental changes. Coral extension has a positive linear relationship with

SST (Lough & Barnes 2000) and air temperature (Bessat & Buigues 2001) until upper or lower physiological thresholds are reached, after which extension rates begin to decline (Edmunds 2005). Lough and Barnes (2000) found that *Porites* extension rates decreased along a latitudinal gradient from North to South on the Great Barrier Reef (GBR), and suggested that coral extension rates were at a historical high due to recent climate change. Numerous laboratory experiments have concluded that decreases in seawater pH (Marubini & Atkinson 1999) and aragonite saturation (Reynaud *et al.* 2003; Marubini *et al.* 2008; Cohen & Holcomb 2009) interfere with coral calcification by reducing available carbonate ions for precipitation, which then reduces extension rates. However, no field evidence is available to support any effect of current rates of ocean acidification on coral growth (Kleypas *et al.* 1999; Cooper *et al.* 2008). Data that describes the relationship between land-based sources of sediment and coral growth rates are lacking (Fabricius 2005; Cooper *et al.* 2008), however, *Porites* on the GBR (Lough & Barnes 1992) and *Montastrea* in the Caribbean (Carricart-Ganivet & Merino 2001) had decreased extension rates with reduced turbidity from inshore to offshore along a gradient of coastal influence. This potentially indicates a positive, though likely indirect, relationship between turbidity and linear extension in corals. Carilli *et al.* (2010) found that coral growth was less resilient to thermal stress when local stressors were present, suggesting that interactive effects between growth, temperature and anthropogenic disturbance occur. Human activity has altered the natural variation in these environmental parameters (e.g. McCulloch *et al.* 2003) through intensified agricultural and industrial development in coastal areas. These human impacts are apparent at different time scales on the GBR, indicating that coral growth responses might only occur during time periods where the changes took place.

European colonization of the GBR catchment began around 1862 (Bureau of Census and Statistics 1975), and though indigenous Australians had used this area for thousands of years (Williams *et al.* 2010), the influence of human activity on the GBR increased dramatically following European settlement (Lewis *et al.* 2007). Land use changes during rapid colonization of northern Queensland have caused a five- to ten-fold increase in sediment flux (McCulloch *et al.* 2003), and an estimated ten- to 20-fold increase in the nutrient enrichment footprint (Wooldridge *et al.* 2006) on the reefs adjacent to the Burdekin River catchment since ~1862. Anthropogenic changes to SST began around 1900 (Cane *et al.* 1997), and Sr/Ca records from the GBR indicate

a 1.3°C increase in mean SST since 1965, with the majority occurring after 1979 (Alibert & McCulloch 1997). Effects on ocean carbonate chemistry on the GBR are relatively recent (0.2-0.3 U change in pH since ~1940, Wei *et al.* 2009), and two recent studies have shown declining growth trends in *Porites* corals since 1988 on the GBR and attributed this decline to SST increases or a decline in aragonite saturation, or both (Cooper *et al.* 2008; De'ath *et al.* 2009).

Inshore coral communities of the GBR have the greatest exposure to the combined effects of land use and anthropogenic climate change due to their proximity to human influence, and this study uses sediment cores of *Goniopora*, a dominant genus in turbid inshore environments, as a new model system. As a result of relatively stable community structure over the length of the cores, a 'stacked' record of *Goniopora* provides the opportunity to examine growth rates beyond the lifespan of a single colony.

The primary aim of this study was to determine whether coral growth rates on the inshore GBR have responded to natural changes in climate, land use impacts associated with European settlement, and more recently, anthropogenic climate change. We hypothesized that *Goniopora* growth rate responses to anthropogenic disturbance are observable in the coral skeleton, given known changes to environmental variables on the GBR and the sensitivity with which coral growth has responded to the environment in previous studies. By examining the 900-year period between 1140 and 2005, we identified pre-European (prior to 1862) baselines of *Goniopora* growth rates and can interpret changes since 1862, and specifically during the period between 1980-2005 when anthropogenic climate change is most pronounced, in the context of an anthropogenically-disturbed environment.

## **Materials and Methods**

Sediment cores of reefs where *Goniopora* spp. corals were dominant over the last 900 years were used to create a time series of changes in growth rates on inshore coral reefs from the Palm Islands in the central GBR. This time series begins in 1140 and continues until 2005, with a 200-year gap between 1390 and 1574.

### *Sample collection*

Sediment cores were collected from the inshore central GBR at Havannah and Pandora reefs, using an open barrel push coring technique (Dardeau *et al.* 2000). In total, 12 cores were collected from each of two sites on the leeward sides of Pandora Reef and Havannah Island, with live *Goniopora* spp.-dominated substrate (Figure 1). At each site, three cores (2-5m), were taken at random intervals along a 20m transect that followed a 5m depth contour across the reef slope. Modern coral fragments were live-collected haphazardly in May 2008 from the two *Goniopora*-dominated sites on Pandora reef. Cores were divided into 5cm sections and the coral fragment contents of each section were separated to maintain age fidelity of specimens after the sediment matrix had been removed. Coral fragments were taxonomically identified to genus, and sections containing *Goniopora* spp. were used for growth rate analysis.

### *Radiometric Dating*

Thermal Ionization Mass Spectrometry (TIMS) U-series age dating, which is based on the ratio of Uranium to Thorium in corals within the cores, was performed at the Radio Isotope Facility (RIF), the University of Queensland (Australia) by Roff (2010), following the methods described by Zhao *et al.* (2009). Corals for U-series dating were sampled from the bases and at various intervals throughout the cores. Reef accretion rates varied but were linear for all cores ( $R^2$  range= 0.92 – 0.99; Roff 2010), and ages at each 5cm section were interpolated using the function determined from fitting a line to available U-series dates for each core. This technique yields an age  $\pm$  standard error (SE) for each 5cm section, with the error being caused by terrigenous sources of Thorium. Average error resulted in a temporal resolution of  $\pm 20$  years per 5cm section (Roff 2010). The median age for each section was assigned to the first year of growth in each coral fragment. As coral fragments varied in age between one and seven years old, radiometric dates were assigned sequentially after the first year and were given the same error values for all ages in each individual fragment.

### *Annual Linear Extension Rate Analysis*

The largest and best-preserved *Goniopora* specimen for each 5cm section where *Goniopora* occurred was selected for acquisition of growth rate data (see robustness analysis section below for testing the effects of fragment size). In total, 383 annual

observations were made from 158 *Goniopora* fragments. Corals were sectioned (7mm thickness) using a guided diamond blade saw, parallel to and including the growth axis of the coral. Sections were placed in an ultrasonic bath for 15 minutes and were oven-dried at 50°C for 15 hours. Corals were digitally X-rayed at 48kV for 2mAs, with a source-to-object distance of 129cm. Sections were ordered randomly on the x-ray sensor to ensure blind analysis, and a metal slide backing was included in the x-ray for scaling calibration.

X-ray images were read and color-enhanced using Osirix software (Rosset *et al.* 2004), and were then converted from DICOM to BMP image files using Adobe Photoshop (see robustness analysis section below for color effects testing). X-ray images were analyzed for annual linear extension rates using CoralXDS software (Helmle *et al.* 2002), which employs a user-defined transect box along the growth axis to identify peak variation in grayscale values that corresponds to annual high-density bands. Annual linear extension was measured as the distance of each high- and low-density band couplet, and the bands were delimited using the second derivative zero method with a cubic spline value of 0.001, following Helmle *et al.* (2002). To minimize measurement error, a box of fixed width was drawn onto the growth axis of each coral specimen (see Figure 2), which acted as a guide for drawing the analytical transect box.

#### *Data Analysis*

Four time periods were selected to differentiate natural variance from that caused by anthropogenic disturbance: full record (1140-2005), pre-European settlement (1140-1862), post-European settlement (1862-2005), and anthropogenic climate change (1980-2005). McCulloch *et al.* (2003) showed abrupt changes in environmental conditions after 1862, which could be reflected in coral growth rates  $\pm 20$  year error, and therefore the origin of colonization ( $\sim 1862$ ) was used as opposed to some period after settlement. The period between 1980 and 2005 was selected to capture any recent climate change effects, as current studies (Cooper *et al.* 2008; De'ath *et al.* 2009) showed that climate change effects on coral growth rates began in the 1980s.

A weighted linear mixed effects model with a nested structure (coral fragment within core within site within reef) was used to analyze the four separate time periods. The

weighting was used to homogenize variance in order to satisfy that assumption of the linear model. Year was treated as a fixed variable, and reef, site, core and fragment were treated as random variables. Random effects in the mixed model increase the power of the analysis, and nesting the spatially hierarchical variables determined whether there is a probable effect of the sampling structure on the results.  $R^2$  values were not reported as  $R^2$  is not well defined for mixed effects models (Gelman & Pardoe 2006). We used a non-parametric kernel regression (with an Epanechnikov kernel) to identify nonlinear relationships between variables and provide detailed nonlinear trends over time (Hastie *et al.* 2009). A 10-year bandwidth was chosen to approximate the average age of a 5cm section of core (Roff 2010) and to coincide with other studies (e.g. Cantin *et al.* 2010). The analysis was repeated with 1-, 2-, 5-, 20-, and 50-year bandwidths and our results are robust to those bandwidths.

Data sets containing proxy reconstructions sourced from corals and sclerosponges of SST (Worheide 1998), pH (Pelejero *et al.* 2005), aragonite saturation (Pelejero *et al.* 2005), sedimentation (McCulloch *et al.* 2003), freshwater discharge (Isdale *et al.* 1998), and SST anomalies (SSTA; Rayner *et al.* 2003) were analyzed for a relationship with extension rates for each of the four time periods. Random effects regressions were used for each factor to detect coinciding temporal trends between annual linear extension rates and each environmental variable throughout the time series. The same technique was used to identify interactions between significant predictors for each time period, but a multiplicative function was used rather than additive. Predicted values were generated for each environmental variable, except linear extension and sedimentation, using a kernel-based local smoothing function with a 10-year bandwidth and zero degree polynomial (i.e. local mean smoothing). This technique generates data for missing periods to enable sufficient statistical power for multiple regressions, and to smooth noise in the distribution for better visualization (Hastie *et al.* 2009). The linear extension and sedimentation datasets are differentiated by reef and year, and therefore, smoothing over year would have distorted individual reef values. Where environmental data exceeded annual frequency, averages were taken to obtain a single value per year. Years of environmental variable data and predicted data when no corresponding *Goniopora* record was available were excluded from analysis. The environmental variables used in these analyses were as geographically and temporally near this study as possible;

however, some disparity exists. An F-test was used to compare residuals of the regression between linear extension and each environmental variable to determine if a significant difference in the relationship exists before and after European settlement. A kernel regression was applied to the strongest environmental predictor of growth rates to identify nonlinear, non-parametric trends in the relationship.

### *Robustness Analysis*

During the initial analyses, consecutive linear extension measurements of the same coral produced different results, and therefore, a standardization procedure addressing the drawing and analyzing components of the software was devised to eliminate this error. The fixed-width box described above (Figure 2) ensured that each transect would be drawn in precisely the same location between measurements, effectively reducing any variation between multiple measurements. Predetermined cubic spline and second derivative values in the analysis component of the CoralXDS program were used to standardize the transect analysis, thereby eliminating bias associated with measurement.

An analysis of multiple brightness and contrast levels was performed to quantify the error introduced by manipulating color values for optimal visualization of the x-rays. To determine whether size of the coral fragment affects growth rates, three measures (length, width, and estimated area [L x W]) of size were analyzed with an Analysis of Variance (ANOVA) as predictors of growth rates. The number of extension rate observations generally increased with time, and in order to test for sample size bias, sample size was regressed with the standard deviation of smoothed values in 10-year bins, which were used in the kernel regressions (described above).

## **Results**

The following sections detail the results of growth rates for each time period: full record (1140-2005), pre-European settlement (1140-1862), post-European settlement (1862-2005), and anthropogenic climate change (1980-2005), as well as the environmental analyses corresponding to each of these time periods. Additional trends in growth rates and the relationship between growth rates and SST are presented as non-parametric regressions.

### *Growth Rate Analysis*

Linear extension rates declined significantly (Table 1) over the full record, from 1.76 cm yr<sup>-1</sup> (SE=0.39, Figure 3) in 1140 to 1.09 cm yr<sup>-1</sup> (SE=0.37) in 2005. The period before European settlement (1140-1862) showed a significant decline from 1.76 cm yr<sup>-1</sup> (SE=0.38) in 1140 to 1.25 cm yr<sup>-1</sup> (SE=0.36) in 1862. Short-term (10-year) trends are visualized with a kernel regression (Figure 4), and a decline in linear extension rates originating around 1600 is apparent. This declining trend continues from 1600 until 2005 with periods of increases and decreases in extension rates that have varying wavelengths and amplitudes. In the period following European settlement between 1862 and 2005, linear extension rates did not change significantly, however, this is due in part to a significant increase in linear extension rates observed between 1980 (0.92 cm yr<sup>-1</sup>, SE=0.37, Figure 5) and 2005 (1.18 cm yr<sup>-1</sup>, SE=0.36) that exceeds all other periods of increase since European settlement (e.g. ~1880-1890 and ~1920-1930, Figure 7). No significant effects of reef, site or core were found for specified time periods except anthropogenic climate change, during which the effects of reef were apparent (Table 2).

### *Environmental Analysis*

Regressions of explanatory environmental variables revealed that SST, river discharge, and sedimentation are significant predictors of linear extension rates for the entire period when growth rates and the covariate data are available (Table 3, Figure 6). Only SST was a significant predictor of growth rates for other time periods, and has a negative relationship with growth following European settlement. Sedimentation also had a negative relationship with linear extension rates, while river discharge had a positive relationship over the full record time period. Aragonite saturation, pH and SSTA did not significantly predict linear extension rates for any time period. A highly significant ( $P < 0.001$ ) difference between before and after European settlement was found in the relationship of linear extension and temperature. Following European settlement, growth rates decline 0.43 cm yr<sup>-1</sup> for every 1°C increase in SST, which is a 48% decrease in the relationship between SST and linear extension from 1862 to 1990. Figure 7 shows a kernel regression plot that suggests a decoupling of SST and growth rate variability around the mid-1800s. No significant differences were found before and after 1862 in the relationship between growth rates and each of river discharge, sedimentation, pH, aragonite saturation and SSTA.

Interactions between significant environmental predictors of growth rates were found for SST and river discharge ( $z=3.01$ ,  $P=0.003$ , coefficient=0.002) for the full record time period only. No interactions were significant predictors of growth rates given SST and sedimentation, sedimentation and river discharge, or SST, sedimentation, and river discharge for any of the four time periods.

### *Robustness Analysis*

In the test for sample size bias, a significant relationship of zero was found (coefficient=0.00008,  $t=3.598$ ,  $P<0.001$ ,) between growth rate variability and sample size, indicating a flat relationship. Therefore, sample size had a negligible effect on kernel regression results. A Cook's distance plot revealed that none of the early (pre-1900) extension rate data points were exerting exceptional influence on the regression results, despite the low number of observations during this portion of the time series. Significant autocorrelation was found in extension rates per year, however, alternative time series structures that would cope with autocorrelation require consecutive years for the entire data set in order to function properly, and this assumption was not met. Therefore, no changes were made to the model based on autocorrelation.

Color bias testing showed error was low ( $SE< 0.5\%$ ) for extreme manipulations of brightness (100% increase and decrease) and contrast (100% increase and decrease), and zero for manipulations representing the enhancement used in this study (25% increase and decrease of contrast and brightness), indicating that minor color adjustments prior to analysis do not impact the extension rate results when using CoralXDS software. No effects of size on growth rates were found (length:  $F=0.238$ ,  $P=0.627$ ; width:  $F=0.8$ ,  $P=0.371$ ; area:  $F=0.238$ ,  $P=0.632$ ).

### **Discussion**

The long-term time series presented here used novel sediment core methods to examine growth rates over a millennial scale, and found that a decline in linear extension rates predated European settlement. The beginning of the decline co-occurs temporally with the cooler sea surface temperatures and intensified ENSO activity of the Little Ice Age (Gergis & Fowler 2009). Environmental analyses showed that over the length of available data, extension rates are primarily driven by sea surface

temperature, and that increases in temperature and rainfall variability may have altered the relationship between SST and coral growth around the time of European settlement, which also coincides with the end of the Little Ice Age (~1870). Extension rates have been in a brief period of recovery from the declining trend since 1980, suggesting that the intensification of anthropogenic pressure on the adjacent catchment during the same period (Australian Bureau of Statistics 2009) is not directly affecting growth rates. These results most strongly support a growth rate response to changes in temperature and rainfall, with limited evidence that anthropogenic changes following European settlement changed the relationship between linear extension and SST. This study provides a valuable historical context for the current concerns about how future climate change will affect coral reefs, and shows that individual coral growth rates have declined over the last 400 years, despite rapid and consistent accretion on these reefs over the last 900 (Roff 2010).

#### *Environmental Effects on Coral Growth*

Few data are available for linear extension rates and explanatory environmental variables prior to 1600 and therefore, identifying the cause of the declining trend in linear extension rates is speculative and based on the co-occurrence in time between changes in growth rates and climate. Higher than average air (Mooney & Maltby 2006) and sea surface (Stott & Kettleborough 2002) temperatures have been reported for the western Pacific during the Medieval Warm Period from 750-1250, during which time coral growth rates were the highest in 900 years. El Niño Southern Oscillation (ENSO) is a dominant driver of climate variability (Markgraf & Diaz 2000), and the period from 1150-1500 is characterized as a transition between baseline variability and persistent El Niño-like climate conditions (Ortlieb *et al.* 2000). Starting around 1300, ENSO intensified, bringing more variable temperatures and periods of drought to Australia, and the end of the 14<sup>th</sup> century marked the start of the Little Ice Age in the southern hemisphere (Kreutz *et al.* 1997). By 1550, ENSO had become highly variable, bringing average 0.2-0.3 °C lower temperatures between 1565 and the end of the Little Ice Age in ~1870 (Hendy *et al.* 2002; Gergis & Fowler 2009). From 1580, growth rates are relatively high and sharply decline almost immediately, coinciding with the first peak in cold periods of the Little Ice Age (Thompson *et al.* 1986). It is plausible that the beginning of the decline in growth

rates around 1600 is due to increasing temperature and rainfall variability caused by ENSO changes.

Field (Lough & Barnes 1997, 2000; Cantin *et al.* 2010) and laboratory (Coles & Jokiel 1978; Marshall & Clode 2004) studies demonstrate the positive non-linear relationship between water temperature and coral extension rates, which occurs until temperature exceeds an upper or lower threshold and growth rates begin to decline. Cantin *et al.* (2010) observed a similar negative response of *Diploastrea heliopora* growth rates to increasing SST in the Red Sea; however, extension rates varied positively with summer SST on 10-year scales until 1995, after which growth rates began a precipitous decline in response to sharply increasing temperatures. In contrast, our results show a continuous negative relationship between growth rates and temperature through the past 900 years that became significantly more pronounced after European settlement. Deconstructing the history of association between SST and coral growth rates, we found that prior to 1862, sea surface temperature does not significantly predict growth rates, but does so after 1862. Given consistent evidence from other studies of a positive relationship between linear extension rates and SST until reaching thermal thresholds, it is unclear why the pre-European relationship between SST and growth rates is negative and insignificant. This disparity between the literature and our results could be due to dating error in one or both of the datasets, or it could reflect the genuine nature of the relationship, but it can be stated conclusively that either a temperature or multiple stressor threshold was reached in the mid 1800s that caused the relationship between SST and growth rates to change.

Sediment flux and river discharge, which also correlate with extension rates for the full record of available data, are inherently related, as terrigenous sediment is delivered to reefs via freshwater river flow (Lewis *et al.* 2007). McCulloch *et al.* (2003) found that coral Ba/Ca sedimentation rates did not show peaks for flood events before 1862, but there was cohesion of large sedimentation peaks for relatively minor flood events shortly after European settlement. This is presented as some of the first evidence to quantify land use change impacts on the GBR catchment associated with European settlement, and indicates that sedimentation on the reefs is caused by other factors in addition to river discharge (McCulloch *et al.* 2003). In addition to European

colonization of the Queensland coast around this time, abrupt changes in oceanic and atmospheric circulation were detected at the end of the Little Ice Age (Kreutz *et al.* 1997). Flood events increased in magnitude and frequency after 1870 (Isdale *et al.* 1998; Lough 2007), though these may be due to natural climate patterns as in the end of the Little Ice Age (Hendy *et al.* 2002), anthropogenic impacts to ENSO patterns of drought (Gergis & Fowler 2009), land use changes in the catchment (McCulloch *et al.* 2003), or a combination therein. The Little Ice Age ended abruptly with higher sea surface temperatures, retreating glaciers and a freshening of the GBR (Hendy *et al.* 2002), in addition to a significantly higher sediment delivery during each rainfall event that was exacerbated by erosion in the catchment (McCulloch *et al.* 2003). The relationship between SST and linear extension rates changed around the time of European settlement, and given the interaction identified between SST and river discharge here, it is possible that these factors synergistically led to a threshold change between linear extension rates and temperature. It is unclear however, whether the changes in climate associated with the end of the Little Ice Age or land use changes characteristic of European settlement are implicated as these events occurred simultaneously.

Despite their functional overlap, river discharge and sedimentation have a positive and negative relationship with growth rate respectively over the length of the record where data were available. Freshwater river discharge lowers salinity and delivers nutrients and sediment to the GBR lagoon. Coles and Jokiel (1978) found that salinity interacts with light and temperature to reduce extension rates in the only study considering salinity effects on coral calcification, contrary to the results found here. Nutrient increases may enhance photosynthesis in corals (Szmant 2002), and have increased extension rates in laboratory experiments (Atkinson *et al.* 1995; Bongiorni *et al.* 2003) and mitigated the negative effects of decreasing aragonite saturation on coral growth rates (Holcomb 2010). Several examples of higher extension rates with closer proximity to river mouths (Lough 1992; Scoffin *et al.* 1992; Carricart-Ganivet & Merino 2001) concur with our results, and when combined with examples of higher extension rates adjacent to sewage outfalls (Lough & Barnes 1997), these studies substantiate that discharged nutrients positively affect coral growth until a threshold of light loss is reached. As Ba/Ca sediment signatures in corals are found in greater intensities than river discharge reconstructions for the same rainfall events

(McCulloch *et al.* 2003), suspended sediments may be more abundant, and cause greater light loss and smothering than nutrient-enriched phytoplankton blooms, thereby reducing extension rates. It is not clear why the relationship between river discharge and growth rates does not significantly intensify following European settlement if land-based nutrient runoff is the mechanism for the positive relationship between these two variables. It is possible that the increased river discharge caused by rainfall is confounded by temperature effects, as higher sea surface temperatures predict more rainfall (Gergis & Fowler 2009), yet we would expect to see a change in the relationship between growth rates and river discharge following European settlement if this was the case.

As each of the reconstructed paleoclimate data sets end in the period between 1980 and 2005, the unexpected increase in extension rates during this time cannot be explained with available data. This time period has 28% of the total variance attributed to reef effects (Table 2), which is likely due to a large number of modern values that were collected from Pandora reef only. It is possible that the increase is part of natural cycles in extension rate trends, though this seems like a poor explanation because this period of increase exceeds all others in length and magnitude since 1862. SSTA derived from instrument records did not have a relationship with coral growth for this period, but a similar analysis using average SST, rather than SSTA, is needed before temperature can be excluded as a causal factor. Farming land use continued to expand between 1980 and 2005 (Bureau of Census and Statistics 1975) and with increasing temperature and rainfall variability, and therefore increased land-based sources of pollution to the reefs, it is expected that growth rates would continue the same growth trend after 1980 as before if land use changes were having a direct effect on growth. That growth rates increased notably during this period despite increasing anthropogenic influence on the Burdekin River suggests that neither sedimentation nor pollution carried to the reef by river discharge alone have been the primary causes of growth rate change, as was hypothesized initially. It can be speculated that a nutrient-enrichment threshold was crossed around this time, supplying corals with critical energy to cope with the thermal stress of historically high sea surface temperatures; effectively creating a positive relationship between SST and growth.

### *Effects of Coral Growth on Reef Growth*

The coral extension rates found in this study are decoupled from accretion rates at the same sites (Figure 8) suggesting that declines in coral growth rates of the dominant reef-builder do not necessarily affect reef accretion, which was found to be rapid and linear for the reefs in this study. The inverse relationship was found by Edinger *et al.* (2000) where net eroding reefs were characterized by high extension rates in massive corals. This study supports the conclusion made by Edinger *et al.* (2000) that individual corals are poor predictors of reef growth, which has implications for both the generality of coral and reef growth relationships, as well as the broader consequences of declining extension rates on reefs. Evidence does not support that current rates of decline in *Goniopora* extension rates affect inshore reefs; although it is likely a different relationship would emerge if a lower threshold of growth rates was reached.

### *Limitations*

Paleoecological data offer a perspective of long-term trends, natural baselines and variability, and information otherwise inaccessible to shorter-term field studies. This study used a remarkably intact record, but it is possible that corals are differentially preserved in sediment, or that multiple fragments came from one colony, which would skew the results, though this is unlikely given known taphonomic processes. It is important, however, that the results of this study are applied with caution, acknowledging the error and bias associated with historical sampling.

Growth rates exhibit a high degree of variability, and as a result, the precise relationship between environmental parameters and extension rates will vary in space, time, and across taxa (Guzman & Cortes 1989; Carricart-Ganivet 2004, 2007). The explanatory variables are a subset of known physical and chemical influences, however, there are potential physical (wave motion, anomalous weather events), chemical (alkalinity, organic and inorganic nutrient availability, toxicity), biological (disease, physiological stress, changes in microbial communities within the coral) and ecological (competition, predation) effects on growth rates for which a mechanism can be explained, and these variables were not analyzed.

### *Conclusions*

This study presents the longest extension rate record in corals yet, and reveals a declining trend in growth rates that predated European settlement as well as a surprising period of recent recovery. Strong relationships between climate variables and *Goniopora* growth rates on the GBR were identified over the length of the time series. It is possible that land use changes in the adjacent catchment indirectly affected growth by altering the relationship between SST and linear extension, or that the recent increase in coral growth rates are due to land-based sources of nutrients, but no conclusive evidence was found.

Future research into this area should focus on elucidating the relationship between specific combinations of stressors and calcification of *in situ* corals. It would also be useful to compare extension rates between severely disturbed and pristine reefs, particularly along a longitudinal gradient of anthropogenic influence. Lastly, research that aims to spatially characterize the suite of growth responses exhibited by different coral taxa would assist in clarifying the natural variability of growth rates.

Figures

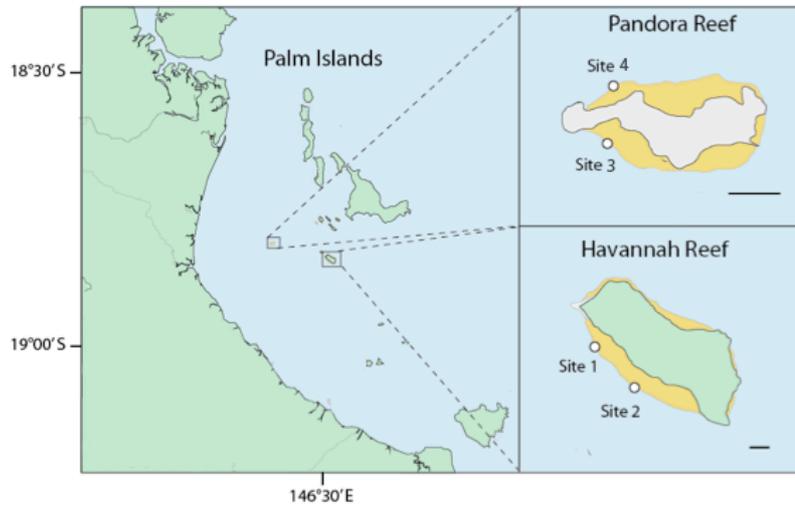


Figure 1. Study sites at Pandora and Havannah reefs (inset) located in the Palm Islands, central Great Barrier Reef, Australia.

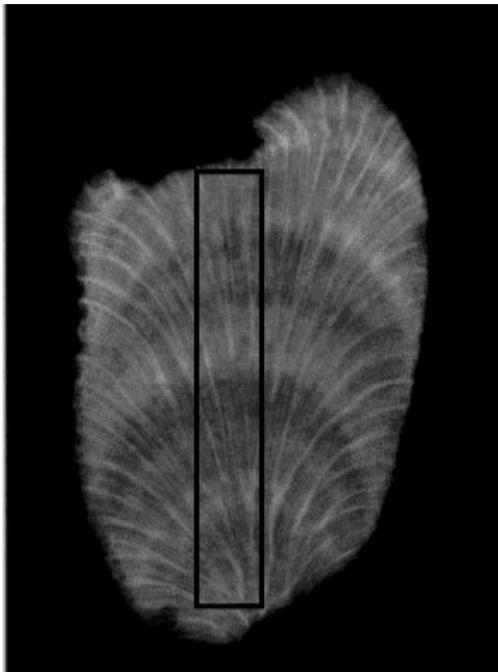


Figure 2. X-radiograph of *Goniopora* specimen and fixed-width box used for drawing consistent transects in CoralXDS for growth rate analysis.

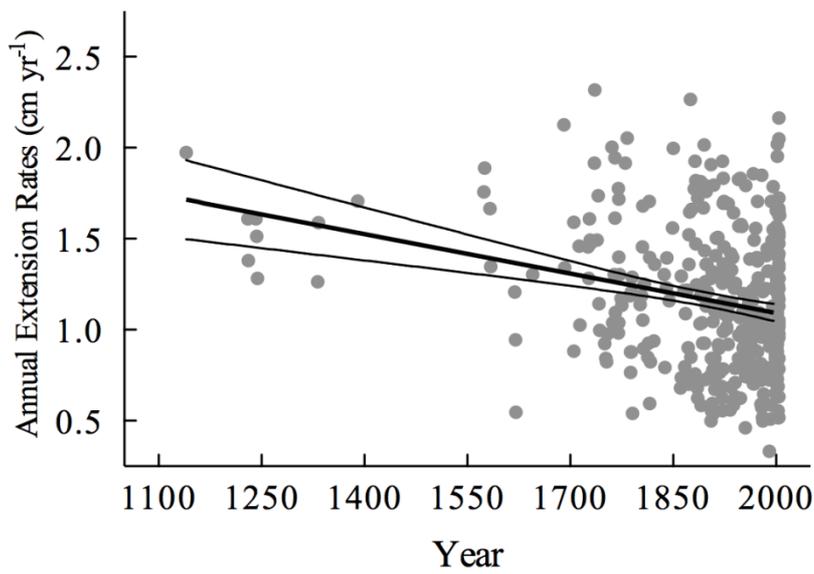


Figure 3. Mean annual *Goniopora* linear extension rates (cm yr<sup>-1</sup>) per year for the full record time period between 1140-2005 with 95% confidence intervals.

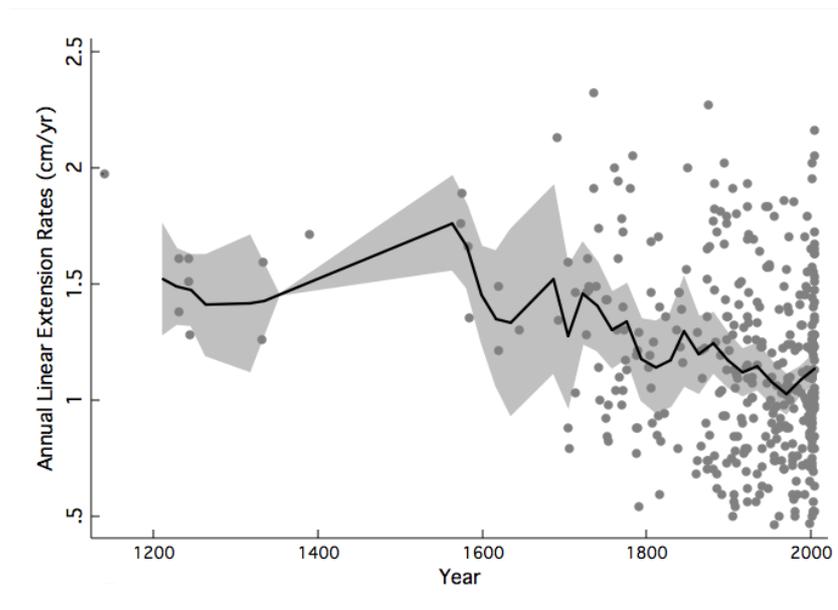


Figure 4. Epanechnikov kernel regression line of annual *Goniopora* linear extension rates over time (1140-2005) using 10-year bandwidths and 95% confidence intervals (shaded area).

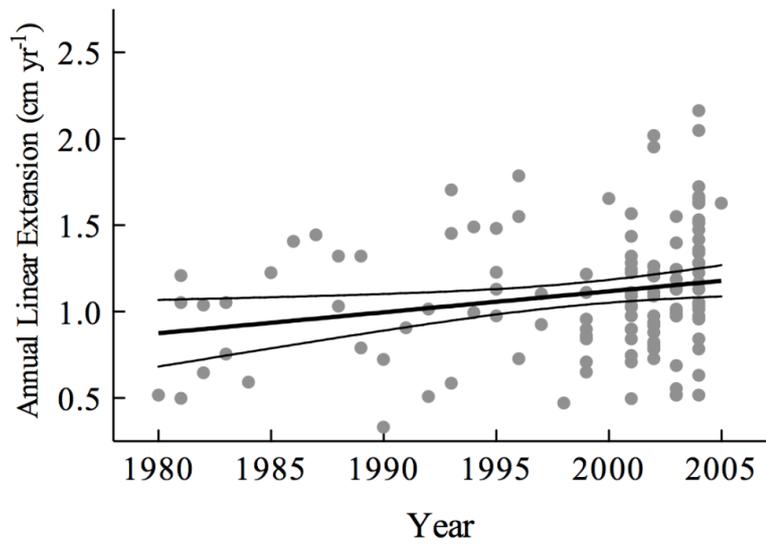


Figure 5. Mean annual *Goniopora* linear extension rates (cm yr<sup>-1</sup>) per year for the anthropogenic climate change period between 1980-2005 with 95% confidence intervals.

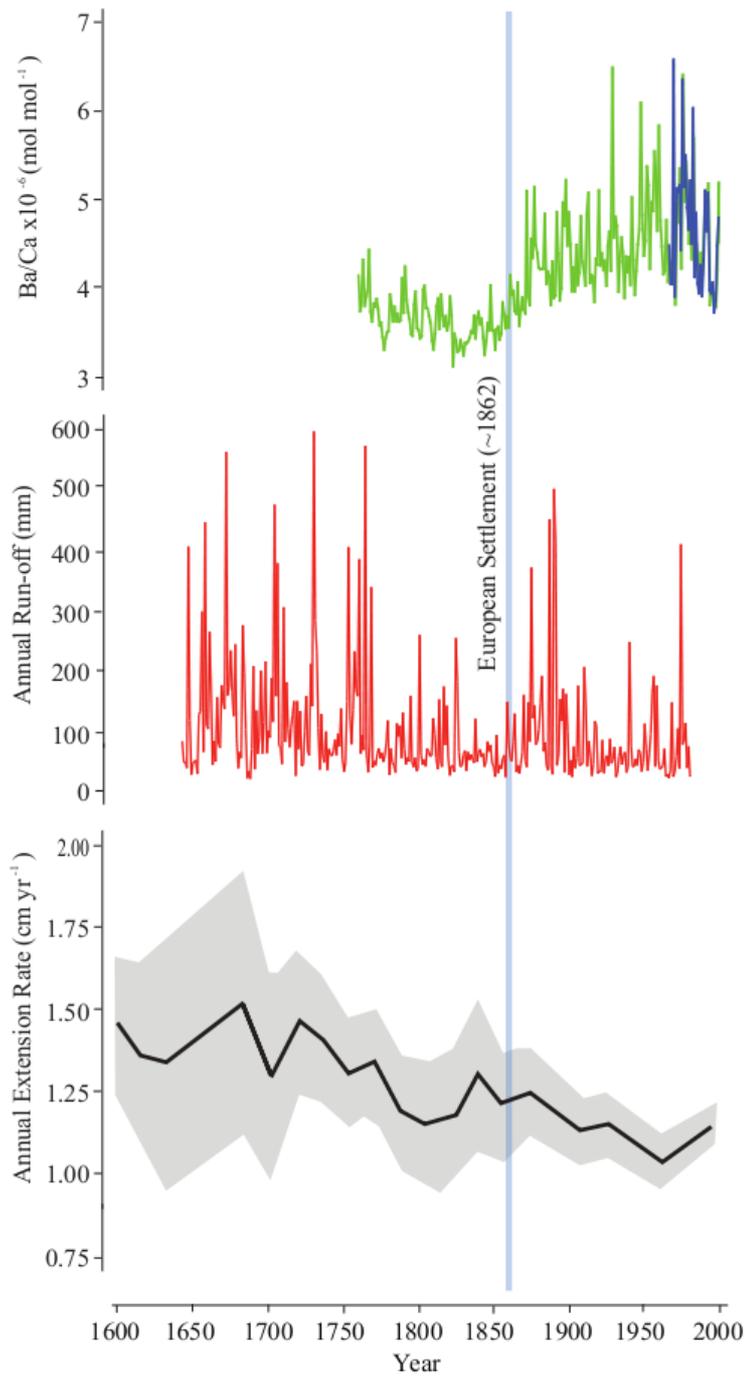


Figure 6. Epanechnikov kernel regressions using 10-year bandwidths of linear extension (black line) with 95% confidence intervals (shaded), a river discharge time series (red line, Isdale *et al.* 1998) and sedimentation (McCulloch *et al.* 2003) at Havannah (green line) and Pandora reefs (blue line).

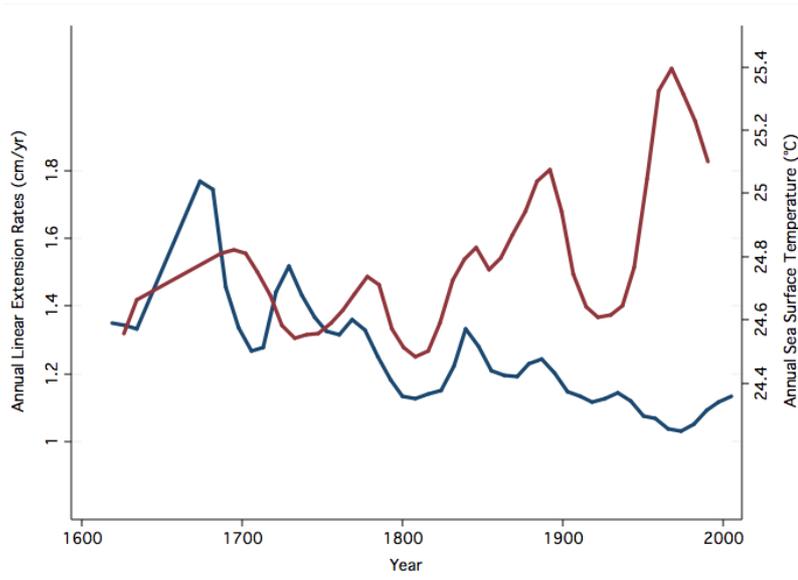


Figure 7. Epanechnikov kernel regressions of SST (red line, Worheide 1998) and annual *Goniopora* linear extension rates (blue line) for the period 1600-2005, using 10-year bandwidths.

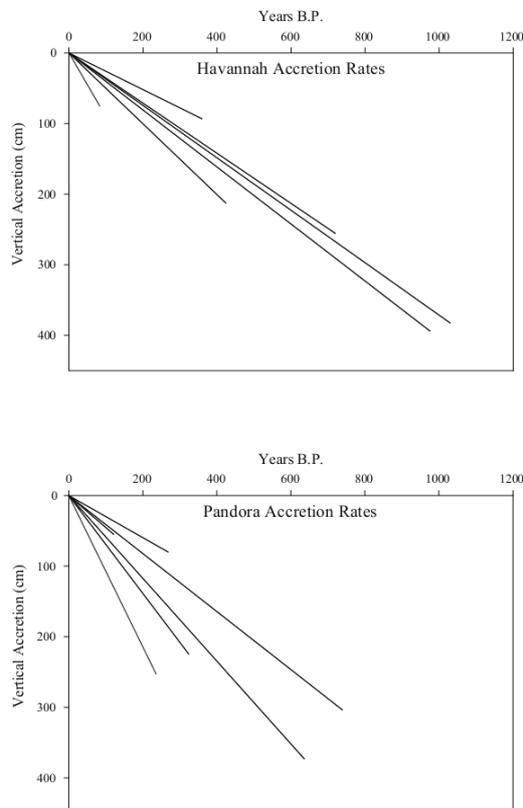


Figure 8. Reef accretion rates ( $\text{cm yr}^{-1}$ ) from Havannah (top) and Pandora (bottom) inshore reef slopes.

Table 1. Summary of *Goniopora* annual linear extension rate analysis results by time period.

Time Period	Period Name	Range cm yr <sup>-1</sup> )	Mean (cm yr <sup>-1</sup> ) ± SE	Sample size (n)	P	Coefficient	DF	t
1140 - 2005	Full record	0.46 – 2.32	1.17±0.02	383	.00006	-0.0008	222	-3.7
1140 - 1862	Pre-European	0.54 – 2.32	1.33±0.04	90	0.03	-0.0007	41	-2.3
1862 - 2005	Post-European	0.56 – 2.27	1.12±0.02	293	0.44	-0.0005	179	-0.8
	Anthropogenic							
1980 - 2005	Climate change	0.47 – 2.16	1.11±0.03	119	0.02	0.0125	75	2

Table 2. Percent variance explained by each nested variable in the mixed-effects model growth rate analysis by time period.

Time Period	%Variance Reef	%Variance Site	%Variance Core	%Variance Fragment
1140 - 2005	0	0	0	100
1140 - 1862	0	0	0	100
1862 - 2005	0	0	2.1	97.9
1980 - 2005	28.4	0	0	71.6

Table 3. Environmental variables regressed against annual linear extension rates per given time period and whether values are predicted or not, what reef the data is derived from and the source of each data set.

Environmental Variables	Time Period	P	z	Coefficient	Predicted	GBR Reefs	Data Period	Source
Sea Surface Temperature	1140-2005	0.000	-4.01	-0.4891	Yes	Ribbon	1554-1990	Worheide 1998
	1140-1861	0.757	0.31	0.2327				
	1862-2005	0.029	-2.18	-0.4333				
	1980-2005	0.352	0.93	6.5612				
Sedimentation	1140-2005	0.026	-2.22	-111254.5	No	Havannah Pandora	1758-1998	McCulloch et al., 2003
	1140-1861	-	-	-				
	1862-2005	0.238	-1.18	-63884.4				
	1980-2005	0.073	-1.80	-201633.5				
River Discharge	1140-2005	0.002	3.04	0.0043	Yes	Havannah Pandora	1644-1980	Isdale et al., 1998
	1140-1861	0.147	1.45	0.003				
	1862-2005	0.277	1.09	0.0045				
	1980-2005	-	-	-				
pH	1140-2005	0.415	0.81	2.3756	Yes	Flinders	1708-1988	Pelejero et al., 2005
	1140-1861	0.825	-0.22	-0.8753				
	1862-2005	0.172	-1.37	-7.6006				
	1980-2005	0.574	-0.56	-17.5957				
Aragonite Saturation	1140-2005	0.894	0.13	0.05102	Yes	Flinders	1708-1988	Pelejero et al., 2005

	1140-1861	0.972	-0.03	-0.0169				
	1862-2005	0.153	1.43	-0.8561				
	1980-2005	0.266	1.11	-9.7189				
SST Anomaly	1140-2005	0.480	0.71	-0.0609	No	Havannah	1863-2005	Rayner et al., 2003
	1140-1861	-	-	-				
	1862-2005	0.439	0.77	-0.0675				
	1980-2005	0.159	1.41	1.1035				

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