1. Tanya M Del Valle, hereby submit this original work as part of the requirements for the degree of Master of Science in Geology.

It is entitled:
Comparative Growth Rates of the Extinct Coral Montastrea nancyi: A Dominant Framework Builder in the Pleistocene (MIS 5e) Reefs of Curaçao, Netherland Antilles

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Committee chair: David Meyer, PhD

Committee member: Carlton Brett, PhD

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Comparative Growth Rates of the Extinct Coral *Montastraea nancyi*: A Dominant Framework Builder in the Pleistocene (MIS 5e)

Reefs of Curaçao, Netherland Antilles

A thesis submitted to the Graduate School of the University of Cincinnati in partial fulfillment of the requirements for the degree of

Master of Arts

in the Department of Geology of the College of Arts and Sciences by

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Abstract

The extinct organ-pipe coral *Montastraea nancyi* Pandolfi was a major framework building coral in reefs of the Pleistocene interglacial highstand (MIS 5e, ~125 kya) in Curaçao as well as many other islands in the Caribbean. In Curaçao well-preserved columns of this species were sampled from two exposures on the windward side of the island and two exposures on the leeward side including both seaward and backreef settings. Columns were slabbed and x-rayed to reveal well-preserved, regularly spaced density bands marking annual growth increments. Measurement of these growth increments provided the first growth rate data for *M. nancyi* from Curaçao, which can be compared to Pleistocene reefs elsewhere in the Caribbean. The mean growth rate (mm, annual linear extension) for both windward localities (6.55-15.49 mm/yr, mean 10.77 mm/yr) was significantly greater than mean growth rate for both leeward sites (5.18-11.32 mm/yr, mean 8.25 mm/yr). The two windward sites did not differ significantly, nor did the two leeward sites, indicating that seaward vs. backreef settings do not differ. The growth rates in Curaçao (5.18-15.49 mm/yr, mean 9.05) fall within the range (8.6 – 16.5 mm/yr, mean 12.6) reported for *M. nancyi* by Holcomb et al. (2004) in Barbados, confirming its ability to achieve high extension rates. Colony sizes for *M. nancyi* in Curaçao are truly spectacular, up to 6 m high on both windward and leeward coasts, extending the full height of the lowest reef terrace formed during the 5e highstand. Considering that this highstand spanned approximately 13 kyr, it is remarkable that the entire reef terrace may have built up in less than 1000 yr. Co-occurring with *M. nancyi* in the Curaçao fossil reefs are colonies of *M. annularis, M. faveolata,* and an unnamed columnar *Montastrea* morphotype similar to that found in Barbados. Well preserved density banding in samples of these taxa of the *Montastrea* species complex will provide further comparisons with the dominant *M. nancyi* in Curaçao and with other Pleistocene Caribbean reefs as well as with extant *Montastrea* species.
Introduction

Globally, modern coral reef ecosystems are on the cusp of rapid environmental and ecologic change. The general perspective of modern coral reef ecosystems is that of a downhill descent from coral domination to algal dominated ecosystems due to multiple anthropogenic influences including climate change, ocean acidification, sea level change, trophic collapse of fisheries with removal of large predators, and pollution (Knowlton et al., 2008). The complexity and negative impact of each of these issues make finding a cause for decline of modern coral reef ecosystems and their significant reduction of coral cover and diversity a challenging imperative for coral reef science.

Skeletal extension rates of coral provide a measurement for reef health that can be linked to a wide range of environmental factors, including climate. Skeletal extension is based on three interrelated environmental factors: the amount of light, water temperature, and water quality or nutrient levels (Johnson et al. 2006). The overall health of a coral reef is dependent upon the ability of the skeletal extension of hermatypic corals to maintain optimum height in the water column despite sea level fluctuations, continual environmental erosion and bio-erosion. (Neumann & Macintyre, 1985)

Most of the information gathered on modern coral reefs has been accumulated in the last half of 20th century thanks to technological advances that made underwater research accessible. However, quantitative data for relative abundance of coral species for any tropical reef beyond four decades are lacking (Pandolfi et al., 2006). Given this limited time span of observation, it is very difficult to predict how coral reefs or individual coral species will react to environmental disturbances such as global climate change and rising sea levels. Furthermore, collected
knowledge of coral reef ecosystems based only on modern reefs is also accompanied by the
dramatic disturbances to the environment caused by overfishing, pollution, and ocean
acidification, the effects of which may have been under appreciated until recently (e.g., Jackson
et al., 2001).

The fossil record, however provides an opportunity to examine the long-term effects of
climate change on coral growth in the absence of anthropogenic factors. Fossil reefs provide a
unique opportunity to study coral reef ecosystems in the past, since they form in place creating
large wave resistant structures that preserve many facets of the community structure and
composition (Pandolfi et al. 2001). The Marine Isotopic Stage 5e, about 125,000 yrs ago
during the last interglacial high-stand, provides an ideal time period for comparison to current
conditions since the MIS 5e was also a period of rising sea level, warmer sea surface temperature
(SST) and global climate change. Greenstein and Curran (1997) confirmed the utility of
Pleistocene fossil coral reef assemblages to record environmental change over long spans of
time. The 125,000 year old Hato Unit of the Lower Terrace Limestone of Curaçao, Netherlands
Antilles exhibits great similarity in patterns of reef species abundance to the current coral reef
ecosystem located offshore and to the pre 1980s reef ecosystem before the most recent
anthropogenic decline (Pandolfi et al. 2001) making it an ideal locality for comparison to the
modern setting. Pandolfi et al. (2001) found the Montastraea species complex to be one of the
dominant hermatypic corals within a diverse community of 39 different coral species in the
Pleistocene fossil coral reefs. The Montastraea species complex includes both extinct and extant
species, allowing for comparison across environmental gradients of leeward and windward
localities as well as a comparison to growth rates of existing species. The two extant species of
Montastraea collected in the present study were M. annularis, and M. faveolata. Although three
species of *Montastraea* species complex were collected from the Hato Unit, this study focuses only on the most abundant and dominant, species *M. nancyi*.

*M. nancyi* is an extinct species from *Montastraea annularis* complex, recognized in 2007 by Pandolfi with type specimens from Barbados. It can be differentiated from other members of the *M. annularis* complex by its distinct organ pipe colony shape, and thin septothecal walls with short costae (Pandolfi 2007) in comparison to *M. faveolata, M. annularis* and *M. franksi*. *M. nancyi* was a long lived coral species ranging from >600Ka to 82Ka (Pandolfi 2007). With an evolutionary life span extending through the interglacial interval of the MIS 5e, *M. nancyi* exhibited an ability to adapt or adjust to dramatic fluctuations in temperature that were at times warmer or cooler than modern conditions in the Curaçao region today. In addition to identifying colonies based on colony shape, Holcomb et al. (2004) used eight distinguishing characters such as corallite fan width and growth angle to identify the members of *M. annularis* complex based on X-radiographs. The methods described by Holcomb were used for identification from x-radiographs in this study. The objectives of this study are to compare
the windward and leeward extension rates of *M.nancyi* in the Pleistocene 5e of Curaçao as well as compare the rates of *M.nancyi* to the modern *Montastraea* complex extension rates of the island.

**Geological setting of study sites**

The island of Curaçao is located in the southern Caribbean Sea, approximately 60 km north of Venezuela. It is 61 km long and 14 km wide. Pleistocene coral reefs in the Lower Terrace Limestone of Curaçao exhibit excellent preservation, perhaps due to low hurricane frequency during the Pleistocene highstand with 93% of colonies in life position (Meyer et al. 2003). Another factor that aided in the excellent preservation is the semi-arid climate with a mean annual temperature of 27°C and rainfall average of 550 mm/yr (Pandolfi et al. 1999; Schellmann, et al. 2004). Tectonic uplift of Curaçao has raised a series of fossil reef terraces above sea level, the youngest being the Hato unit of the Lower Terrace exposed along the entire perimeter of the island. The Hato unit was dated to approximately 125,000 yrs BP using radiometric dating and stratigraphic relationships by Herweijer and Focke (1978). On average, about 6 m of the Lower Terrace Hato unit is exposed at the four localities in this study. The windward (NE) side of the island is exposed to tradewinds of ~5m/s (Pandolfi et al. 1999) creating a higher energy wave environment. The leeward side of the island from the NW to SE experiences a low energy wave environment (Pandolfi et al. 2001)

Figure 3. Boca Patrick fore-reef (left) to back-reef (right).
Coastal exposures of the Hato Unit of the Lower Terrace were chosen to allow for comparison of windward (high wave energy) and leeward (low energy) environments. Figure 2 shows the four principal localities. Windward localities were Boca Patrick (Fig. 3) and Boca Wandomi (Fig. 4), and on the leeward coast, localities were at Santa Marta Bay (Fig. 5) and Playa Forti (Fig. 6). Boca Wandomi and Boca Patrick provide complete reef sequences from forereef to back reef, perpendicular to the present coastline, exposed in erosional channels incised during the sea level drop of the Last Glacial Maximum (Herweijer & Focke, 1978). On the leeward side, the Playa Forti section runs parallel to the present shoreline and exposes the seaward margin of the Pleistocene reef. The section at Santa Marta Bay is located with an inner bay and was protected by a ridge of older, uplifted Pleistocene carbonates that indicate a back reef or bay environment.

Environments among the four localities vary and therefore environment cannot be held as a constant for all localities in the comparisons. Boca Patrick and Boca Wandomi are similar environments in that they are cross-sections from seaward to landward of the windward. However the sampled colonies at Boca Patrick and Boca Wandomi are not the exact same distance from the seaward side, because some were located further inward. On the leeward side, Playa Forti is a seaward reef and is comparable to the windward sites. Santa Marta is a back-bay setting and
therefore different from all the other sites. Age for all four localities is fixed as these are all from the Pleistocene 5e time interval, during the rise of sea level.

Figure 5 Santa Marta Bay. A) Aerial view. B) Outcrop along inner bay, seaward side to left. C) Large *M.nancyi* colony D) Individual specimens of *M.nancyi*. E) Close up of *M.nancyi* candlebra or organ pipe shaped colony.
Figure 6. Playa Forti. Large colony of *M. nancyi* representing less than 1,000 years of reef accretion.
Methods

Sclerochronology, the study of skeletal extension rates uses the “linear distance between consecutive top edges of high density band portions” (Dodge et al., 1977) to represent growth for one year (Hudson et al., 1976). Coral samples are cut parallel to the axis of coral growth into 5mm slabs. The samples were then x-rayed using an Americomp Spectra 325e model with a Toshiba X-ray tube at 40-45 KV 200 MA for 1/40 second. The x-rays were scanned and converted into JPEGs at 600 dpi. Using the morphometric software program TPSdigs provided by SUNY, a dot was placed at the top of each high-density band and the linear distance was measured between each band and its consecutive neighbor along the longest possible transect through each sample. Each individual transect was along a colony of a single species of coral. There are several samples along a transect of a single colony (Fig. SM1). Note, however, that in sample cutting preparation and shipping that small segments were lost. Nevertheless, transects represent a collection of nearly continuous yearly extension rates throughout the life span of a single colony. All statistics were calculated using the statistical program SAS.
Results

The extinct *Montastraea nancyi* samples collected from Curaçao show well preserved high and low density bands similar to those observed in modern *Montastraea*. Based on this study, annual skeletal extension rates for the extinct *M. nancyi* on Curaçao range from 5.18 to 15.49 mm/year (mean 9.05 mm/yr, SD 3.85 with 95% CI 0.35).

Windward Localities

The annual skeletal extension rate of *M. nancyi* for localities on the windward side of the island ranges from 6.55 – 15.49 mm/yr with a 95% CI of 0.77 and a mean of 10.77 mm/yr. No means of means were used. Table 1 provides the transect mean extension rate, SD, 95% CI and SE. Table 1 (Supplementary Material) provides the raw data of each sample, including mean extension, SD, 95% CI and SE. Annual extension rates for Boca Patrick range from 6.11 to 15.61 mm/yr with a mean of 10.86 and a 95% CI of 0.91 (Fig. 8). Annual extension rates for Boca Wandomi range from 5.86 to 15.18 mm/yr with a mean of 10.86 and 95% CI of 1.53. There is no statistical difference in the variation of skeletal extension rates between the two windward localities (ANOVA df=2, F= 0.2599, P = 0.77, α= .05, Table 1).
Leeward Localities

The annual skeletal extension rate for the leeward side of the island ranges from 5.18 to 11.32 mm/yr with a 95% CI of 0.34 and a mean of 8.25 mm/yr. Annual extension rates for Santa Marta Bay range from 5.20 to 10.90 mm/yr with mean of 8.05 and a 95% CI of 0.86. Refer to Figure 8. Refer to Supplementary Material Table 1 for individual transect data.

Annual extension rates for Playa Forti, based on the three different transects, are 5.17 to 11.40 mm/yr with a mean of 8.29 and a 95% CI of 0.37 (Fig. 8, Table 1). There is no statistical difference in the variation of skeletal extension rates between the two leeward localities (ANOVA df=2, F=0.2599, P = 0.77, α=.05).

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Table 1 Mean Annual Extension of *M. nancyi* by Transect on Curaçao
Figure 8. A) Skeletal extension (mean and 95% CI) of *M. nancyi* in Curaçao at all 4 localities. B) Skeletal extension (mean and 95% CI) of *M. nancyi*, in aggregate, on the leeward and windward side of Curaçao.
Windward vs. Leeward

Using a nested ANOVA analysis, the variation in skeletal extension rates was compared by locality, transect and sample. The mean skeletal extension for *M. nancyi* on the windward sites is 10.77 mm/yr with 95 CI% of 0.77. The mean skeletal extension for the leeward sites is 8.25 mm/yr with 95% CI of 0.34. There is a statistically significant difference in skeletal extension rates between the windward and leeward sides of the island (ANOVA df = 1, F = 61.93, P = 2.87E-14, α = .05, Table 1).

Discussion

Growth rates in Curaçao fall within the range 8.6 – 16.5 mm/yr (mean 12.6) reported for *M. nancyi* by Pandolfi in 2007 from specimens collected in Barbados, confirming its ability to achieve high extension rates. These high extension rates contributed to *M. nancyi* being a dominant coral in the Pleistocene reef community as noted by Pandolfi et al. in 2001. It should also be noted that there may be an unintentional sampling bias because samples were taken from the largest colonies available. These would have been the longest lived, healthiest colonies. Consequently the extension rates should be viewed as maximal. Information on individual specimens with mean, 95% CI and SD can be found in Table 1 of the Supplementary Information.

The climatic variations of the MIS 5e enabled a luxuriant and diverse reef with 39 species (Pandolfi et al., 2001) to form in Curaçao 125,000 years ago. During MIS 5e, ice sheets retreated globally and sea level rose 3 – 6 m above present level. According to Medley et al. (2008) Sea Surface Temperature (SST) was 1.5°C higher during MIS 5e than present temperatures in the
Cariaco Basin near Venezuela (close to the study site). Statistically significant differences in skeletal extension rates between the leeward (mean of 8.25mm/yr) and windward (mean of 10.77mm/yr) sides could be related to several factors, such as increased turbulence, food availability, or sediment removal due to the effects of the easterly tradewinds that were similar in position and strength to the modern easterly tradewinds. Previous studies of reef diversity and reef development have shown peaks in diversity coincide with breaks in the slope along the forereef slope, and it is there that turbulence is maximized, thus preventing sediment deposition. (Porter, 1972). It is possible that due to less sediment deposition that M.nancyi could have a higher extension rate. The leeward side of the island receives reduced wave energy relative to the windward side in part due to the position of the nearby Island of Bonaire ~50 km to the southeast (Pandolfi et al.,2001). While the leeward reefs of the Pleistocene resemble the modern leeward reefs in Curaçao, the windward reefs are significantly deeper (>12m) at present. This difference in reef depth was caused by tectonic uplift and changes in the island profile since the Pleistocene 125,000 yrs. ago (Pandolfi et al., 2001) The difference in environments made it difficult to make a comparison to the modern leeward and windward skeletal extension rates in Curaçao for extant species of the genus Montastraea.

The only other data on skeletal extension rates for the extinct species M. nancyi were reported by Holcomb et al. (2004) and Pandolfi (2007) from the Pleistocene uplifted reefs of Barbados, where extension rates ranged from 8.6 – 16.5 mm/yr , with a mean of 12.6 mm/yr. Annual skeletal extension rates for M.nancyi on Curaçao range from 5.18 to 15.49mm/ year, with an overall mean of 9.05 mm/yr, closely overlapping the range reported for Barbados.

Mean skeletal extension rates for Montastraea from the Key Largo Limestone of south Florida was reported by Gischler et al (2009) to be 5.2mm/yr. Although the Key Largo reefs
were also formed during MIS 5e (ca. 125Ka), they represent shallow patch reefs rather than the exposed outer reefs of the Hato Unit of Curacao. Gischler et al (2009) suggested that the lower growth rates in the Key Largo may have resulted from SST higher than present and the effect of El Niño-Southern Oscillation climate variations during the Pleistocene Interglacial Stage 5e. It should also be noted that Gischler et al. (2009) identified their samples as *M. annularis* (sensu lato) and did not refer them to *M. nancyi* or any other *Montastraea* species that are now recognized to comprise a species complex (Holcomb et al., 2004).

Van Veghel (1995) reported growth rates for living *Montastraea* on Curacao, also based on X-radiographs of annual density banding. Extension rates range from 5.24 - 11.55 mm/yr for three morphotypes corresponding to the presently recognized species *M. annularis* ss, *M. faveolata*, and *M. franksi*. Van Veghel used three morphotypes to distinguish the *Montastraea* complex, which were bumpy, massive and columnar. Bumpy, which is equivalent to *M. franksi* had a significantly lower growth rate of 4.4 to 6.3 mm/yr than the other two. Massive, which corresponds to *M. faveolata* had extension rates of 9.3 mm/yr. Columnar which is identifiable as *M. annularis* had extension rates of 10.6- 12.9 mm/yr. *M. faveolata* (massive) and *M.annularis* (columnar) were significantly different in only one case. As reported here, growth rates of *M. nancyi* ranged from 5.18 to 15.49mm/ yr during the Pleistocene MIS 5e, suggesting that *M. nancyi* may have had a higher growth potential than the modern *Montastraea complex*.

The mean annual mean growth rate 9.05 mm/yr for *M. nancyi* in Curacao during MIS 5e indicates that colonies like that at Playa Forti (Fig. 6) that extend to the full height of the Lower Terrace (~ 6m) could have built up in approximately 663 years meaning the Lower Terrace as exposed could well represent less than 1000 yr of reef accretion. However the entire MIS 5e extended at least 13,000 yrs. Thus the entire reef might represent only a fraction of that time of
sea level rise. The ability of *M. nancyi* for rapid skeletal extension in times of sea level fluctuation without a doubt attributed to its survival through the Pleistocene and the longevity of the species, which ranged from 600K to 82K (Pandolfi, 2007).

With the ability to endure sea level fluctuations and climatic changes, the reason why *M. nancyi* went extinct remains unanswered. Research being currently in progress by Dennis Hubbard and Ann Budd on samples collected in the Dominican Republic may greatly extend the range of this species to possibly 10,000K and provide insight on its extinction date, which may be related to hybridization with other members of the *Montastraea* complex and the difficulty of identifying hybrid fossil coral. The research by Hubbard and Budd is currently being conducted and will provide further insights into this topic, though at this time is not yet published.
Conclusions

1. Pleistocene *M. nancyi* in the Curaçao displayed a wide variation in annual growth rates with high annual skeletal extension rates as noted in the type specimens from Barbados.

2. Annual skeletal extension rates for *M. nancyi* on Curaçao range from 5.18 to 15.49mm/ year with a mean 9.05, SD 3.85 and 0.35 95%CI.

3. There is a statistically significant difference in skeletal extension rates between the windward and leeward sides of the island.

4. There is no statistical difference between the two leeward localities or between the two windward localities.

5. The high skeletal extension rate, large colony size and length of species range from >600ka to 82ka show the ability of *M. nancyi* to persist and prosper despite the rising sea levels, changing SST, and climatic variability.
References


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Reefs During Glacioeustatic Sea-Level Fall, Great Inagua Island, Bahamas: Geological Society of America Special Papers, v. 300, p. 51-61
Supplementary Material

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Table 1. Mean Annual Extension for individual specimens of *M. nancyi* in Curaçao
Figure 1 Boxplot of *M. nancyi* annual extension rates in Curaçao by locality
Figure 2 Boxplot of annual extension rates of *M. nancyi* in Curaçao by transect Santa Marta 1-2, Playa Forti 3-7, Boca Patrick 8, Boca Wandomi 9-10