Invited research article

# Expanded Florida reef development during the mid-Pliocene warm period

James S. Klaus [a,*], John F. Meeder [b], Donald F. McNeill [a], Jon F. Woodhead [c], Peter K. Swart [a]

[a] Department of Marine Geosciences, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA
[b] Southeast Environmental Research Center, Florida International University, Miami, FL 33199, USA
[c] School of Earth Sciences, University of Melbourne, Parkville, Victoria 3010, Australia

## ARTICLE INFO

## ABSTRACT

The coral fauna of the Tamiami Formation documents a northern expansion of reef development along the Florida Peninsula during the mid-Pliocene warm period (MPWP). Radiometric dating (U-Pb) of *Solenastrea bournoni* produced an age of $2.99 \pm 0.11$ Ma, constraining reef development to the MPWP and the peak of Plio-Pleistocene faunal turnover; subsequent to the final closure of the Central American Seaway (CAS) but prior to major Northern Hemisphere Glaciation (NHG). Coral faunal analyses are based on a total of 1614 coral specimens collected along a 165 km stretch of the west Florida coast, and included rarefaction and detrended correspondence analysis (DCA). A total of 60 coral species occur within the Tamiami Formation, with faunal assemblages ranging from 42 to 87% extinct taxa. The Tamiami collections can be split into a southern "reef" assemblage with high diversity of stenotopic taxa and a northern "non-reef" assemblage with lower diversity eurytopic taxa. The southern reef assemblage contains framework buildups of the dominant tropical taxa *Stylophora affinis*, *Orbicella annularis*, and *Acropora cervicornis*. We interpret enhanced west Florida reef development during the middle Pliocene to be a product of more equitable sea surface temperatures, and reduced salinity fluctuations associated with higher sea levels. While mean sea surface temperature estimates based on oxygen isotopic analysis of the coral *Solenastrea bournoni* (25.3 °C) are similar to present day values (26 °C), a completely flooded southern Florida Platform in the Pliocene would be less prone to salinity fluctuations associated with coastal runoff and extreme cold-water events during winter storms. While higher latitude range shifts of tropical reef corals associated with current global climate change have been documented elsewhere in the world, we do not foresee the West Florida Shelf being conducive to significant range shifts in tropical coral taxa or reef development within the coming century.

## 1. Introduction

Coral reefs have changed dramatically over recent decades as a result of human overexploitation, pollution, and global climate change (Hughes et al., 2003; Pandolfi et al., 2003). Since climate warming is forecast to continue, predicting the impact of climate change on the abundance and distribution of reef corals has become relevant in establishing conservation priorities (Roberts et al., 2002; Brooks et al., 2006; Pandolfi, 2015). Most studies of climate change effects on corals have focused on temperature-induced coral bleaching and mass mortality in tropical areas. Optimum temperatures for coral growth are generally around 26–27 °C (Clausen and Roth, 1975; Jokiel and Coles, 1977; Marshall and Clode, 2004). While bleaching thresholds vary by region and can be influenced by other environmental factors (light, salinity, biological), they typically range between 28.3 and 30.2 °C (Hoegh-

Guldberg, 1999). Extreme cold water can also influence photosynthetic efficiency, and result in coral bleaching and mortality (Saxby et al., 2003; Hoegh-Guldberg et al., 2005; Lirman et al., 2011). Cold-temperature tolerances are not well defined for corals, but early experiments show that prolonged exposure to 16 °C is stressful to most species and that exposure to temperatures of 14 °C for as little as 9 h can result in coral mortality (Mayor, 1914; Mayor, 1918; Muscatine et al., 1991). The present-day global distribution of coral reefs generally coincides with the 18 °C monthly minimum seawater isotherm (Kleypas et al., 1999).

Average global sea surface temperatures are rising at a rate of 0.11 °C per decade (Rhein et al., 2013). While future increases may result in increased tropical bleaching, they may also result in poleward range shifts or expansions into temperate areas as lethal low temperature thresholds shift to higher latitudes. Evidence of the poleward range expansion of modern corals has been documented along the east coast of Australia (Baird et al., 2012), as well as the temperate areas of Japan (Takatsuki et al., 2007, Yamano et al., 2011). Coral range expansions have also

been detected in the recent geologic past. Precht and Aronson (2004) documented an expanded northern limit of two cold-sensitive species, *Acropora palmata* and *Acropora cervicornis*, along the Florida east coast during the middle Holocene (10,000–6000 years ago), while Greenstein and Pandolfi (2008) document expanded ranges of tropical taxa along the coast of western Australia during the last interglacial period.

The modern coral fauna of the West Florida shelf is generally impoverished with minimal framework reef development (Hine et al., 2008). Here we document expanded reef development within the region during the mid-Pliocene warm period (MPWP). The MPWP ranges from 3.3 to 2.9 Ma, and is increasingly recognized as an important analog for future climate change (Robinson et al., 2008; Haywood et al., 2009). The MPWP represents the last time atmospheric $CO_2$ concentrations were in the range 350 to 450 ppm (Pagani et al., 2011). Model–data comparisons suggest that mean surface temperature was warmer than pre-industrial for the average interglacial climate state during the MPWP (Dowsett et al., 2012; Haywood et al., 2013). Global mean sea surface temperature (SST) is estimated at +1.7 °C above the 1901–1920 mean based on large data syntheses (Lunt et al., 2010; Dowsett et al., 2012), and general circulation model (GCM) results agree with this SST anomaly to within ±0.5 °C (Haywood et al., 2013).

Coral collections were made from the Tamiami Formation exposed between Naples and Sarasota along the west coast of Florida (Fig. 1). Faunal records were analyzed in combination with previously well-sampled Neogene coral localities of the Caribbean region to determine the pattern and timing of Neogene faunal changes, and to interpret the role of community structure in Plio-Pleistocene regional extinctions. We assess the environmental factors that may have contributed to diverse high-latitude reef development along the Florida Platform, and consider whether the Tamiami Formation provides a reasonable analog for expanded coral ranges and reef development associated with future climate change within this century.



Fig. 1. Regional Map of southern Florida showing coral collection localities.

## 2. Regional geology

The Tamiami Formation was first described by Mansfield (1939) as the Tamiami limestone. The name was proposed for fossiliferous, sandy limestones exposed at the surface and along the canal and borrow pits adjacent to the Tamiami Trail (U.S. 41) in Monroe and Collier Counties. Hunter (1968) formally proposed five lithostratigraphic members (Ochopee limestone member, Buckingham limestone member, Pinecrest sand member, Murdock Station member, and Bayshore Clay member) of the Tamiami Formation and placed the members into three successive concurrent range zones. Meeder (1979a) recognized a capping coralline-rich limestone in Collier and Lee Counties, Florida, later named the Golden Gate Reef member of the Tamiami Formation (Meeder, 1979b). The Golden Gate Reef member overlies skeletal sands of the Ochopee limestone, and was described as having two reef intervals separated by a distinct discontinuity surface. The top of the Golden Gate Reef member is an irregular surface exhibiting jointing, solution pipes, accretionary laminated crusts, root casts, and (dis)solution breccia. Based on Sr isotope analyses within core W-16242 near Sanibel Island, Missimer (2002) constrained the entire 35 m thick Tamiami Formation to between 4.95 and 1.95 Ma.

## 3. Materials and methods

### 3.1. U-Pb chemistry and mass spectrometry

The U-Pb method can be extremely useful in providing critical age constraints on relatively pristine materials that lie beyond the range of the U-Th chronometer (e.g. Denniston et al., 2008; Quigley et al., 2012). A widely recognized impediment to the U-Th dating of young corals is the susceptibility of their porous and metastable aragonite skeletons to open system behavior resulting in mobility of U or intermediate U-series daughter products. The exact nature of these processes is still much debated with no current consensus (Scholtz and Mangini, 2006). Despite the potential for open system behavior, if U-Pb isochrons can be obtained, it necessarily implies that any possible open-system behavior in the U-decay chain occurred relatively soon after deposition and was not long-lived. Furthermore, it is also important to note that most of the effects observed in the U-Th dating of corals lie well within the typical uncertainty bounds of U-Pb age determinations. An integrated approach was used to assess the potential for diagenetic alteration in our coral sample prior to dating, including: petrographic thin sectioning and electron microscopy (SEM), X-ray diffraction (XRD), and the stable isotopes of carbon and oxygen (see methods below).

We applied U-Pb geochronology to a single exceptionally preserved specimen of *Solenastrea bournoni* (CCD-54102) collected from the Tamiami Formation at locality CFOO3. No other corals from our collection were deemed suitable for age dating or other geochemical analyses. The analytical methods employed in this study follow closely those published previously by Woodhead et al. (2006). Isotope ratios were determined on a Nu© Plasma MC-ICPMS using a DSN-100 desolvation unit and MicroMist glass nebuliser, operating in the range 50–100 μl/min uptake. Instrumental mass bias effects were monitored and corrected using NIST SRM 981 reference material in the case of Pb, and the sample's internal $^{238}U/^{235}U$ ratio (=137.88) in the case of U. $^{238}U/^{206}Pb$–$^{207}Pb/^{206}Pb$ ages were calculated using the intersection of the isochron with an appropriate concordia, accounting for initial disequilibrium in the $^{238}U$ and $^{235}U$ decay chains (and employing a modern seawater $^{234}U/^{238}U$ ratio).

### 3.2. Petrographic and scanning electron microscopy

Standard petrographic microscopy and SEM were used to assess pristine coral preservation through the presence of coral micromorphological features such as teeth and denticles as well as microstructural calcification centers and radiating bundles of aragonitic fibers.
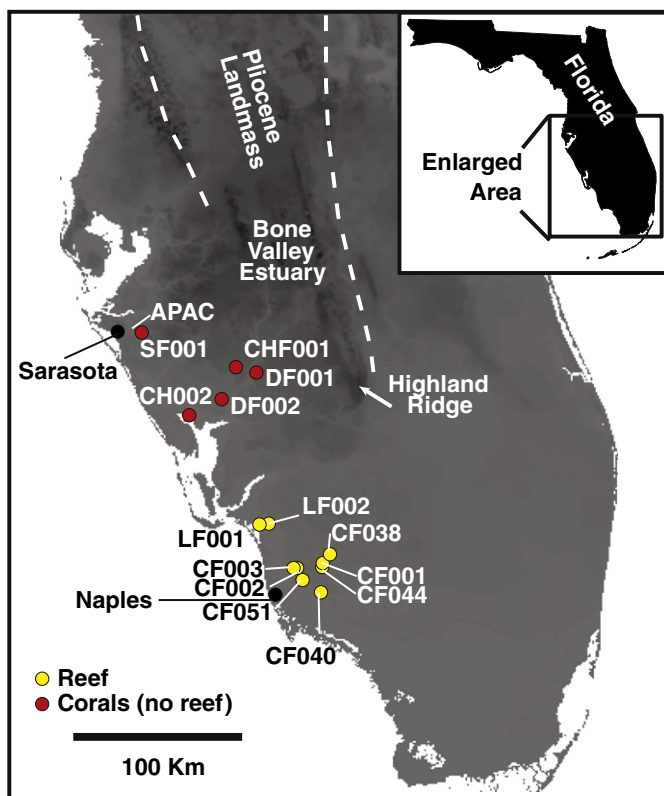
Petrographic microscopy and SEM were also used to assess the presence of secondary pore-lining cements. SEM samples are sputter coated with palladium and examined with a Philips XL-30 environmental SEM.

### 3.3. X-ray diffraction

To assess pristine preservation, the bulk carbonate mineralogy for *S. bournoni* specimen CCD-54102 was determined using XRD. Pristine modern coral samples with no secondary recrystallization or pore-lining cements are typically 100% aragonite (Milliman, 1974). Homogenized samples from the coral skeleton are made into a paste, and mounted onto glass slides. Relative percentages of carbonate minerals are determined by comparison of peak area ratios of samples and a set of standards composed of known mixtures of carbonate minerals. Peak areas are determined using the electronic X-ray counter on a Panalytical XRD. An integrated count for each peak is made, and counts of background X-ray levels are subtracted from each peak.

### 3.4. Stable isotopes

A total of 139 powders were drilled in a linear transect across six annual density bands in a cut slab of *S. bournoni* specimen CCD-54102. The $\delta^{13}C$ and $\delta^{18}O$ values of the skeletons were measured using a Kiel III automated device interfaced with a Thermo-Finnigan© Delta Plus mass spectrometer. All data are corrected for the usual isobaric interferences and reported relative to Vienna Pee Dee Belemnite (V-PDB) in the conventional notation. Error associated with the measurement of stable inorganic $\delta^{13}C$ and $\delta^{18}O$ compositions is <0.1‰. To aid interpretation, the data were compared to two previously published records from modern *Solenastrea* specimens from south Florida (Swart et al., 1996) and four other Pliocene specimens previously analyzed from the Tamiami Formation (Roulier and Quinn, 1995; Brachert et al., 2016).

### 3.5. Coral collections

Coral collections were made at 14 localities along the west coast of Florida between Naples and Sarasota (Fig. 1, SI_Table S1). The majority of collected specimens came from six primary localities (CF001, CF002, DF001, LF001, CF002, CHF001). All coral specimens of this collection were deposited in the University of Miami Paleontology Repository, and have been identified using a standard set of characters and character states developed on the basis of morphometric analyses of Neogene and Recent samples collected across the Caribbean region (Budd et al., 1994). Illustrations of diagnostic characters from each species are available from the Neogene Biota of Tropical America taxonomic database (NMITA: http://nmita.geology.uiowa.edu). Although the corals were generally very well preserved, aside from *S. bournoni* specimen CCD-54102, they were not suitable for geochemical analysis.

### 3.6. Rarefaction analysis

Rarefaction curves were used to assess both the relative sampling intensity, as well as the relative diversity among the six most heavily sampled assemblages. Rarefaction curves were generated using the software program EstimateS (Colwell, 2013).

### 3.7. Detrended correspondence analysis

In order to determine the similarity of the Tamiami Formation assemblages to other Neogene Caribbean coral assemblages, and assess latitudinal differences as well as the timing of Neogene community change, we compiled a relative abundance occurrence matrix of 46 well-sampled assemblages from throughout the Caribbean (Budd et al., 1996; Budd et al., 1998; Budd and McNeill, 1998; Budd et al., 1999; Klaus et al., 2008; Klaus et al., 2012). We analyzed the occurrence matrix through detrended correspondence analysis (DCA) with the
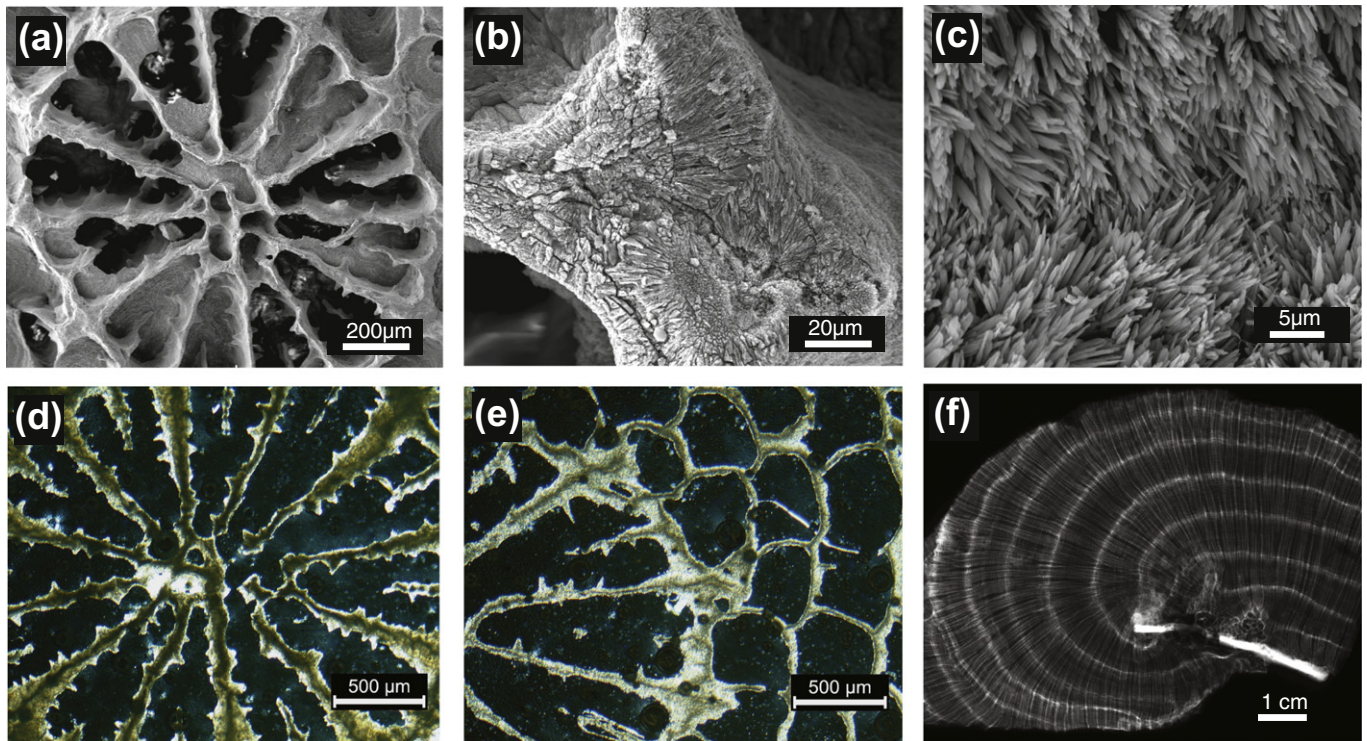


Fig. 2. (a–c) SEM micrograph of corallite from *S. bournoni* specimen CCD-54102 showing preservation of septal ornamentation, calcification centers, and aragonite trabeculae. (d–e) Thin section micrographs of specimen CCD-54102 showing calcification centers and an absence of pore-lining cements. (f) X-rayed slab of specimen CCD-54102 showing annual high density banding.

software package PAST v.3.05 (Hammer et al., 2001). We chose DCA because of the large heterogeneity in the dataset (gradient length >4) and because many species deviated from a linear response model. Analysis by DCA is one of the most effective at removing edge and arch effects from gradient data. (Legendre and Legendre, 1998; ter Braak and Šmilauer, 2002).

## 4. Results

### 4.1. Coral preservation, geochemistry and U-Pb age constraint

An integrated approach was used to assess diagenetic alteration and suitability for closed-system U-Pb radiometric dating of *S. bournoni* specimen CCD-54102 collected from locality CFOO3. Petrographic thin section, SEM, and X-ray micrographs reveal detailed preservation of micro-morphological features such as teeth and denticles (Fig. 2a, d, e) as well as micro-structural calcification centers, radiating bundles of aragonitic fibers, and annual density banding (Fig. 2b–f). Furthermore, no significant secondary pore-lining cements or sediment infilling was observed below the outer growth surface (Fig. 2d–e). X-ray diffraction profiles from three replicate samples revealed 100% aragonite. The $\delta^{13}C$ values from 139 replicate samples ranged from −1.1 to −5.8‰ while values of $\delta^{18}O$ ranged from −1.5 to −5.0‰ (Fig. 3). For comparison we plot the mean $\delta^{18}O$ and $\delta^{13}C$ values of specimen CCD-54102 with other modern (Swart et al., 1996) and Pliocene (Roulier and Quinn, 1995; Brachert et al., 2016) *Solenastrea* samples analyzed from Florida (Fig. 4). In comparison to the modern samples, values of $\delta^{18}O$ were most similar to the specimen collected from the east coast of Broward County (Swart et al., 1996), while the $\delta^{13}C$ values were more similar to the modern sample from Florida Bay. In comparison to other Pliocene *Solenastrea*, values of both $\delta^{18}O$ and $\delta^{13}C$ were most



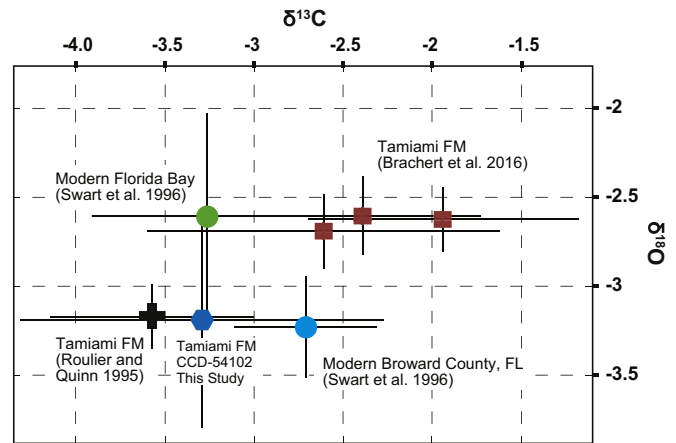**Fig. 4.** $\delta^{13}C$ and $\delta^{18}O$ data from *S. bournoni* specimen CCD-54102 compared to modern *S. bournoni* specimens from Florida Bay and Broward County, Florida (Swart et al., 1996) as well as other *S. bournoni* from the Tamiami Formation (Roulier and Quinn, 1995; Brachert et al., 2016).

similar to the Roulier and Quinn (1995) specimen collected from the APAC shell mine near present day Sarasota. Samples exposed to meteoric diagenesis typically display $\delta^{13}C$ values between −2.0 to −12.0‰ and $\delta^{18}O$ values between −3.0 to −6.0‰ and follow the inverted-J model of Lohmann (1988) (Swart, 2015).

Based on analysis of nine subsamples, a $^{238}U/^{206}Pb–^{207}Pb/^{206}Pb$ Tera-Wasserburg concordia age of 2.99 ± 0.11 Ma (2σ) was obtained (Fig. 5). The fact that a U-Pb isochron was obtained, necessarily implies that any possible open-system behavior in the U-decay chain occurred relatively soon after deposition and was not long-lived.

### 4.2. Tamiami Formation coral fauna

A total of 1614 coral specimens (SI_Table S2) were collected from 14 localities (Fig. 1, SI_Table S1) of the Tamiami Formation. The collections contain a total of 32 genera and 60 coral species (SI_Table S2, Fig. 6). Of the 60 species identified, 26 are extinct and 5 are known only from the
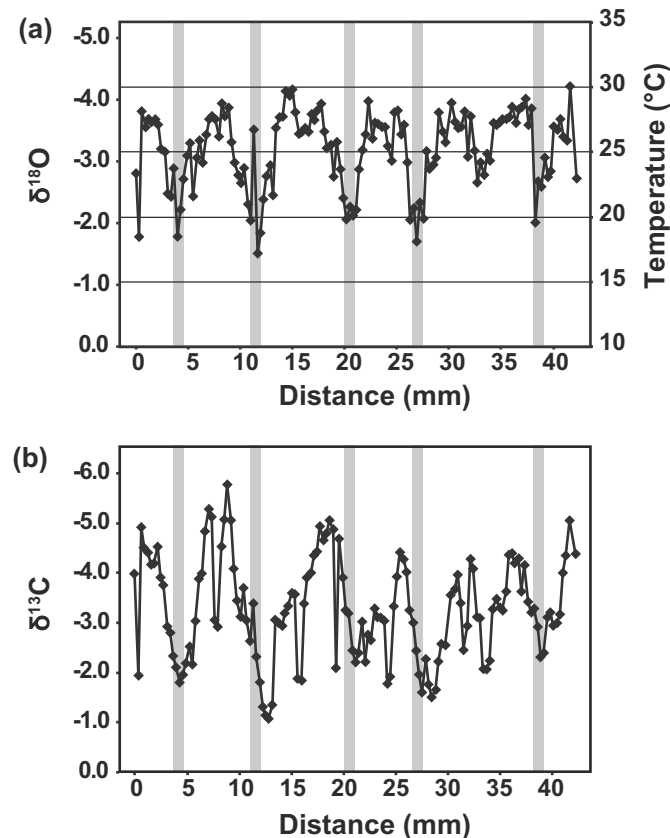


**Fig. 3.** (a) Six year serial record of $\delta^{18}O$, and temperature from *S. bournoni* specimen CCD-54102. (b) Corresponding six year record of $\delta^{13}C$.
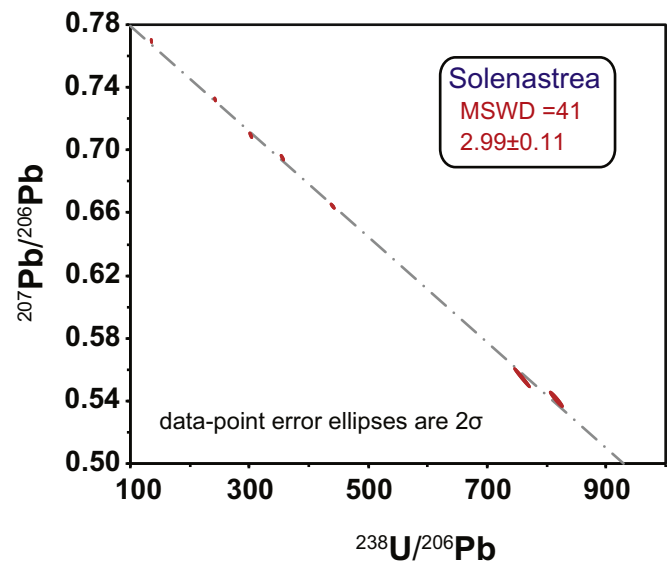


**Fig. 5.** $^{238}U/^{206}Pb$ versus $^{207}Pb/^{206}Pb$ concordia plot showing sample aliquots measured in *S. bournoni* specimen CCD-54102 of the Tamiami Formation and used to obtain a Tera-Wasserburg concordia age of 2.99 ± 0.11 Ma (2σ).
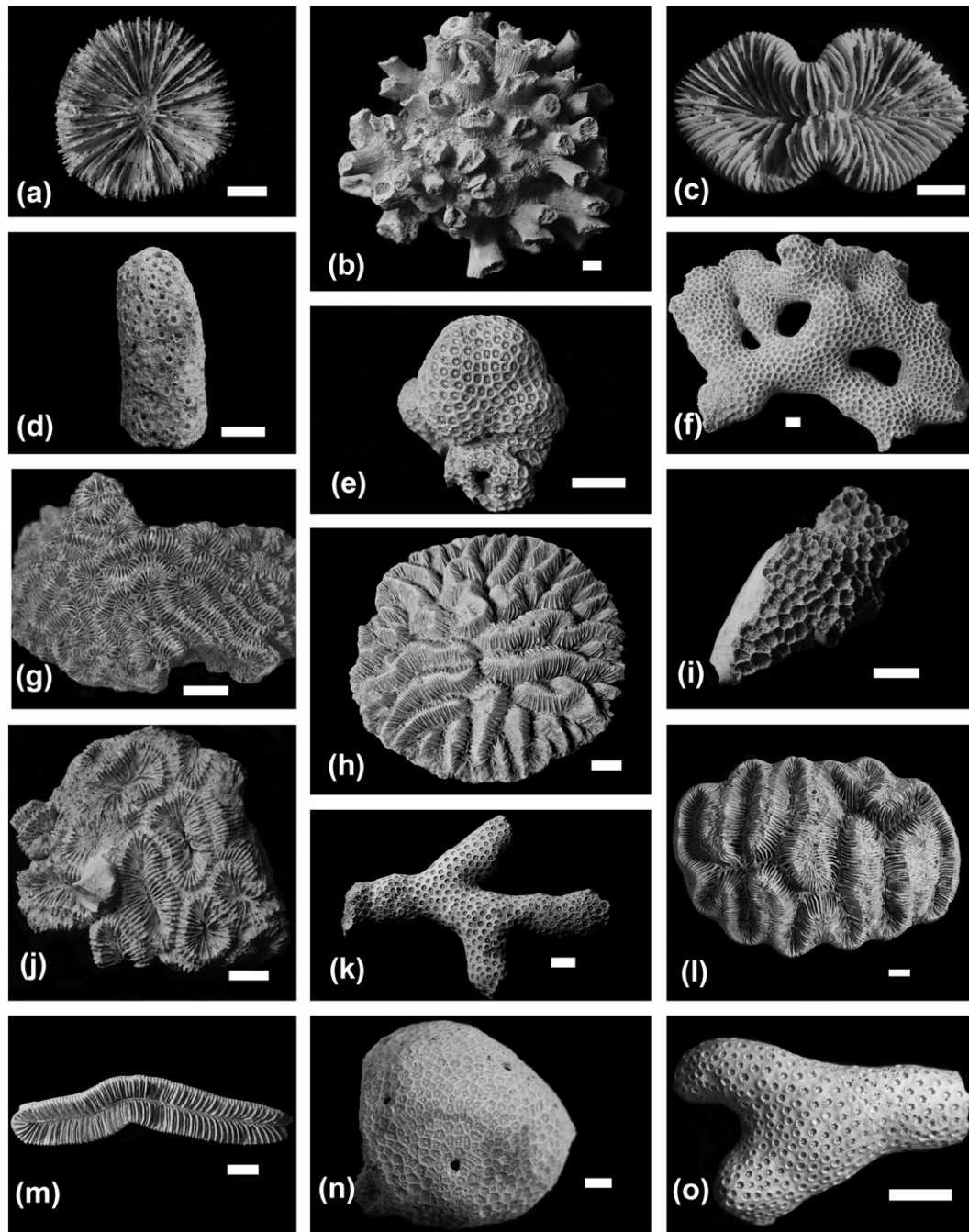
**Fig. 6.** Common Neogene coral species recovered from the Tamiami Formation along the west coast of Florida. (a) *Scolymia lacera* (CCD-53546, CF001, scale bar 1 cm). (b) *Dichocoenia eminens* (CCD-53796, DF001, scale bar 1 cm). (c) *Trachyphyllia bilobata* (CCD-54489, CF001, scale bar 1 cm). (d) *Acropora cervicornis* (CCD-53558, CF001, scale bar 1 cm). (e) *Madracis decactis* (CCD-54489, CF001, scale bar 1 cm). (f) *Septastrea crassa* (CCD-54203, CHF001, scale bar 1 cm). (g) *Pseudodiploria sarasotana* (CCD-54543, DF002, scale bar 1 cm). (h) *Meandrina meandrites* (CCD-54610, CF003, scale bar 1 cm). (i) *Septastrea marylandica* (CCD-53822, CF001, scale bar 1 cm). (j) *Mussismilia hispida* (CCD-54048, CF001, scale bar 1 cm). (k) *Oculina sarasotana* (CCD-54610, CF003, scale bar 1 cm). (l) *Manicina areolata* (CCD-53000, CF002, scale bar 1 cm). (m) *Placocyathus alveolus* (CCD-53897, CF001, scale bar 1 cm). (n) *Siderastrea pliocenica* (CCD-53840, DC001, scale bar 1 cm). (o) *Stylophora granulata* (CCD-53942, CF001, scale bar 1 cm).

Tamiami Formation (*Pseudodiploria sarasotana* [Weisbord, 1974], *Oculina sarasotana* [Weisbord, 1974], *Siderastrea dalli* [Weisbord, 1974] *Scolymia* sp.A, and *Scolymia* sp.B).

Of the 1614 specimens collected, 1482 came from 6 primary collecting localities. Rarefaction curves for each of the six localities suggest additional species would likely be recovered with additional sampling (Fig. 7a). Based on present sampling, the rarefaction curves also suggest higher richness within the CF001 and LF001 assemblages, intermediate richness within the CF002 and CF003 assemblages, and lower richness in the DF001 and CHF001 assemblages. The six Tamiami assemblages ranged between 38% and 55% extinct taxa, which comprised between 42% and 87% of the specimens within the assemblages (Fig. 7b).

Assemblages CF001, CF002, CF003, and LF001 located in the southern half of the study area are the most taxonomically diverse assemblages (Fig. 8a–d) and form expansive flat-bottom coral carpets with localized reefal buildups (coralline framework, topographic relief). These localities show a mix of branching, massive, free-living, platy
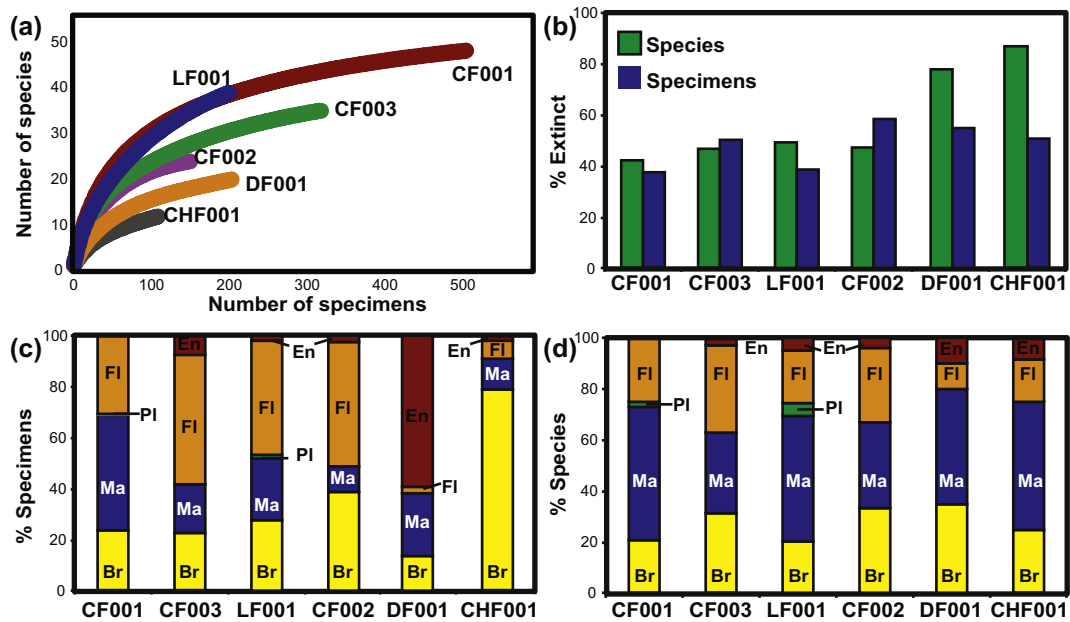
**Fig. 7.** (a) Rarefaction curves showing the estimated number of coral species based on sampling intensity within each of the six Tamiami assemblages. (b) Bar chart showing the relative percentage of extant taxa within each of the six sampled reefs. (c) Bar chart showing the relative abundance coral colony growth forms (Br = branching, Ma = massive, Pl = plate, Fl = free-living, En = encrusting) based on the total number of specimens collected from the six assemblages. (d) Bar chart showing the relative abundance of coral colony growth forms based on the species collected from the six reefs.

and encrusting species (Fig. 7c–d). While there is variability between sites, dominant taxa include the branching species *Stylophora affinis* (Fig. 6o), and *Porites porites*, massive species *S. bournoni* (Fig. 2), *Orbicella annularis*, and *P. strigosa*, and free-living species *Trachyphyllia*

*bilobata* (Fig. 6c), *Placocyathus costatus*, and *Manicina areolata*. The two northern assemblages, DF001 and CHF001, are less diverse and do not show evidence for reefal buildup. These assemblages are dominated by two species from the genera *Septastrea* (Fig. 8e–f). Assemblage
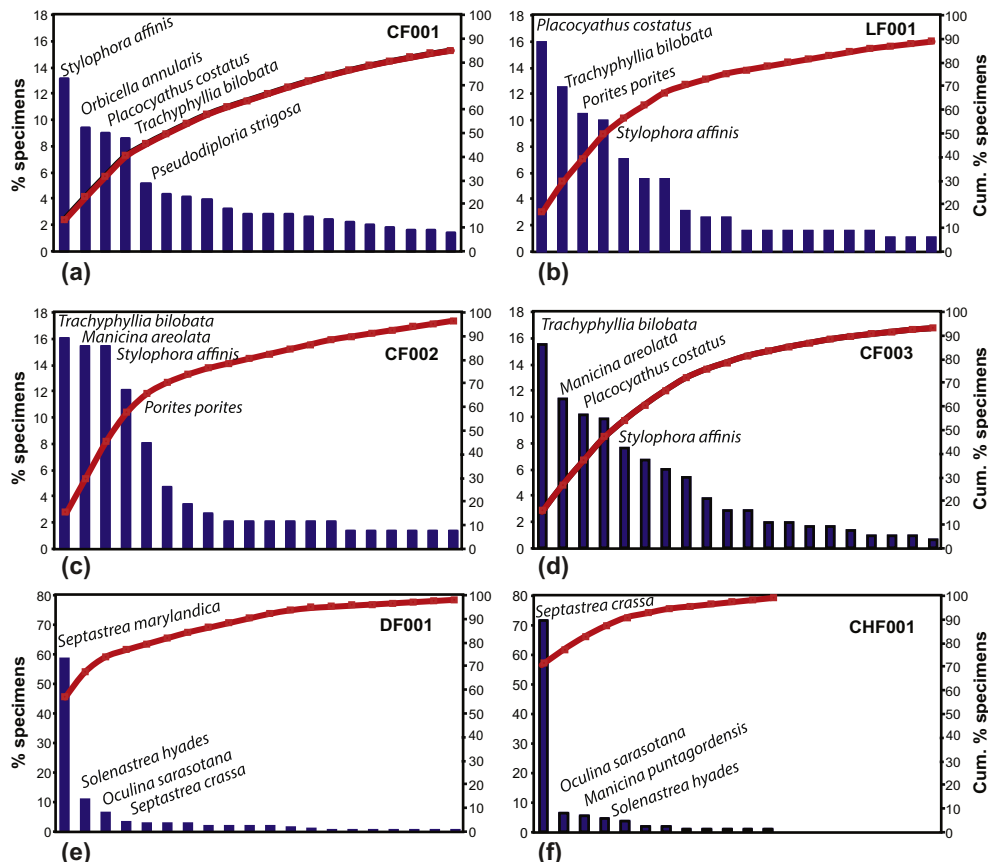


**Fig. 8.** (a–f) Percent abundance and cumulative abundance plots for the six well-sampled localities of the Tamiami Formation.

DF001 is dominated by the encrusting species *Septastrea marylandica* (Fig. 6i) while assemblage CHF001 is dominated by the branching species *Septastrea crassa* (Fig. 6f). Other common taxa from the northern localities include the massive coral *Solenastrea hyades*, the branching coral *O. sarasotana* (Fig. 6k), and the free-living coral *Manicina puntagordensis*.

### 4.3. Comparison to other Neogene reef assemblages

Ordination by detrended correspondence analysis (DCA) was performed on a coral relative abundance matrix assembled from 46 well-sampled Late Miocene to Late Pleistocene coral assemblages. Results of the DCA analysis suggest a generalized trend along Axis 2 related to geologic time (Fig. 9). Older Late Miocene assemblages have low values, while younger Late Pleistocene assemblages have higher values. Exceptions to this trend are the two assemblages from the Bowden Formation, Jamaica (BW1, BW2), which have lower values on Axis 2 than might be expected for their Late Pliocene age. The Bowden assemblages (Budd and McNeill, 1998) contain a large number of free-living taxa, similar to the older Cibao Basin assemblages of Dominican Republic (Klaus et al., 2008; Klaus et al., 2011). In contrast, the Late Pliocene Quebrada Chocolate (QC2) assemblage (Budd et al., 1999) has slightly higher values along axis 2 than might be expected for their Late Pliocene age. The QC2 assemblage clusters with a number of Early Pleistocene assemblages, and is characterized by abundant extant taxa.

The Tamiami Formation assemblages cluster in an age appropriate position along DCA Axis 2, above the Late Miocene and Early Pliocene assemblages of the Dominican Republic and below the Early Pleistocene assemblages from Curaçao, Jamaica, Costa Rica and Panama. Along DCA Axis 1, the Tamiami Formation assemblages are clearly anomalous from the lower latitude Caribbean assemblages. Although the southern Tamiami reefal assemblages are more similar to the Caribbean assemblages than the northern non-reefal assemblages, they are also clearly outliers. This is evident even after removing the northern localities from the ordination. The Tamiami Formation is most clearly distinguished from the overall Caribbean trend by the presence of *S. crassa*, *S. marylandica*, *Mussismilia hispida*, and the endemic taxa *P. sarasotana*, *O. sarasotana*, *S. dalli*, *S.* sp.A, and *S.* sp.B.

## 5. Discussion

### 5.1. Environmental controls on modern reef development

The west Florida continental shelf is characterized as a distally-steepened, carbonate ramp platform (Hine et al., 2008); lacking a ridge of reefs, shoals, and islands that define a rimmed platform such as Belize or south of the Florida Keys. Prolific shallow-water reef development on the West Florida Shelf is thought to be limited by a number of factors including sea surface temperatures, salinity fluctuations, current patterns, benthic substrate, and periodic disturbance events (Jaap, 2015). Based on the NOAA Buoy network, average monthly seawater temperatures ranged from 22 to 31 °C at the Dry Tortugas and 18–30 °C near Tampa. Both Smith (1954) and Glynn (1973) argued that the 21 °C isotherm in January represented the northern limits of "coral reef development" in the Gulf of Mexico. Arguably more important than the average monthly temperatures, during cooling associated with polar frontal passages, waters of shallow bays and nearshore waters can drop below 10 °C, triggering widespread bleaching events (Lirman et al., 2011). The impact of polar fronts on seawater temperatures of the West Florida Shelf is highlighted in Fig. 10.

Based on coral latitudinal distribution, Jaap (2015) subdivided the West Florida Shelf into zoogeographic sub-regions. The region seaward of Key West to the Dry Tortugas and approximately 25 km northward to Harbor Keys is characterized by a diverse Caribbean fauna. North of this sub-region, the major reef building genera, *Acropora*, *Orbicella*, *Pseudodiploria*, and *Colpophyllia* are either missing or extremely rare. From Naples northward to the Florida Middle Grounds, the fauna becomes principally eurytopic taxa (*Cladocora*, *Manicina*, *Isophyllia*, *Scolymia*, *Siderastrea* and *Oculina*). The offshore Florida Middle Grounds is moderately more diverse including *Madracis decactis*, *Dichocoenia stokesi*, *Meandrites meandrites*, and *Porites branneri* (Jaap, 2015 and references therein).

The coral taxa off the east coast of Florida (Miami to Fort Lauderdale) include the reef builders *A. cervicornis*, and *A. palmata* (Vargas-Ángel et al., 2003; Precht and Aronson, 2004). These reef-building species extend further northwards along the east coast due to the Florida Current and poleward transport of warm water. In contrast, the West Florida Shelf has weak ocean currents and the Loop Current is rarely in a position to support larval transport into the nearshore areas of the eastern Gulf of Mexico. Aside from filaments that may occasionally intrude into shallower water, the Loop Current is typically west of the 100 m depth contour (Cooper et al., 1990).

### 5.2. Environmental controls on expanded Pliocene reef development

The high diversity reefs of the Tamiami Formation clearly reflect a change in environmental conditions from the present day West Florida Shelf. The highest diversity framework reefs with numerous stenotopic coral taxa were found near Naples while lower diversity coral biostromes characterized by more subtropical and eurytopic taxa were found at the more northerly localities between Naples and Sarasota. A number of taxa with relatively high lowest survival temperatures
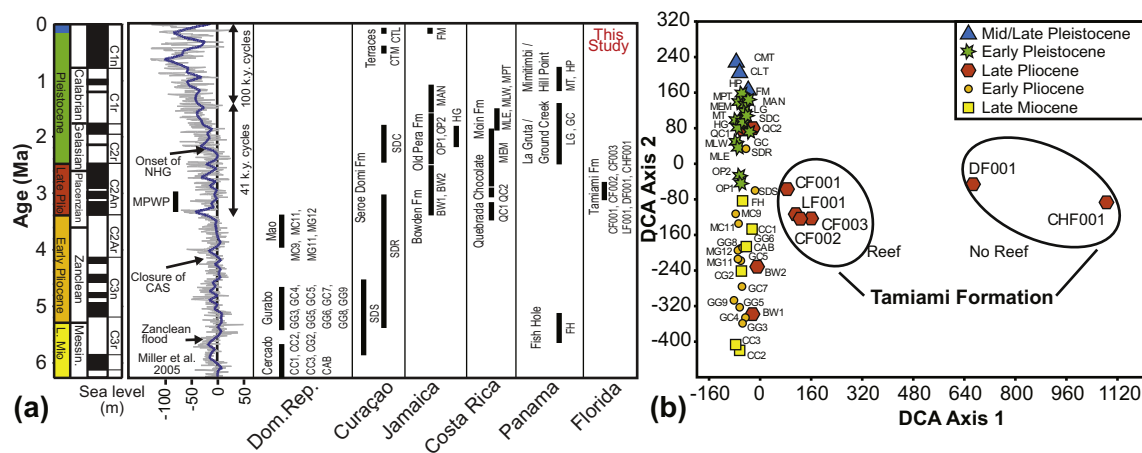


**Fig. 9.** (a) Geologic ranges of well-sampled Caribbean reef coral faunas included in detrended correspondence analysis (DCA). (b) Ordination of 46 Neogene zooxanthellate coral assemblages (6.25–0.10 Ma) based on detrended correspondence analysis (DCA) of relative abundance data.
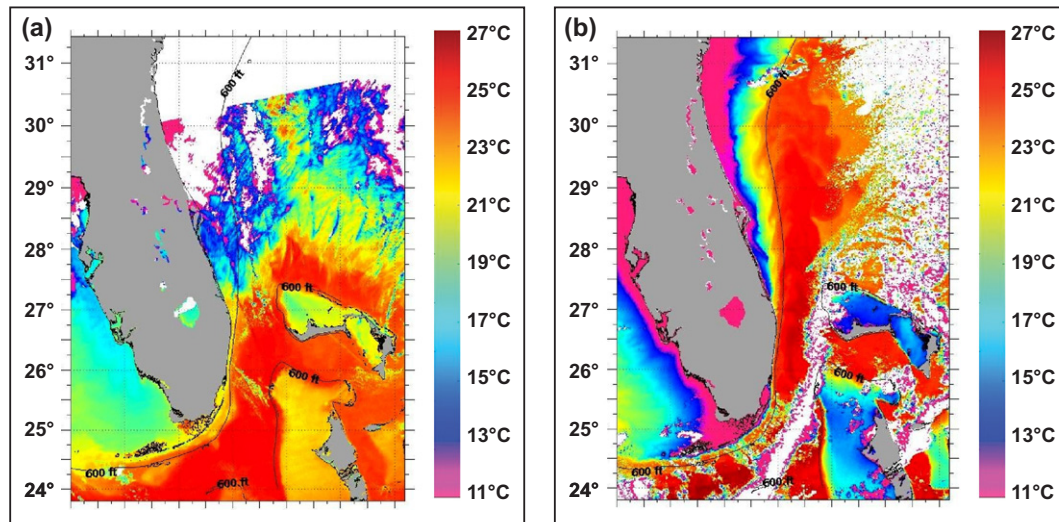
**Fig. 10.** Maps showing SST of south Florida during typical winter conditions (a), and during a winter cold front (b). Sea surface temperature imagery is from the NOAA Advanced Very High Resolution Radiometer (AVHRR) satellites and the Rutgers University Coastal Ocean Observation Laboratory.

(LST) were found within the Tamiami Formation (*A. cervicornis* LST = 14.1, *O. annularis* LST = 16, *P Pseudodiploria clivosa* LST = 15.3) (Mayor, 1914; Mayor, 1918).

The warm water stenotopic coral fauna of the Tamiami Formation is consistent with data suggesting mean global surface temperature was + 1.7 °C warmer during the MPWP (Lunt et al., 2010; Dowsett et al., 2012; Haywood et al., 2013). However, attempts to reconstruct paleo-SST for the Tamiami Formation have returned estimates that are typically less than present day SST. Most temperature estimates for the Tamiami Formation have been conducted from or near the "Pincrest Beds" of the APAC, Inc. Shell Pit near Sarasota, Florida. For example, estimates based on ostracod transfer functions and modern analog techniques suggest average temperatures of 18–25 °C (Cronin, 1991; Willard et al., 1993). This is approximately 3–5 °C less than the present day. However, Cronin and Dowsett (1996) speculated that these estimates may be biased by the absence of brackish water taxa in the transfer function database. Roulier and Quinn (1995) estimated similar mean annual SST for the Pincrest Beds (20.5–22.5 °C) based on stable isotopic records from the fossil coral *S. bournoni*, whereas Jones and Allmon (1995) estimated even lower temperatures (15–24 °C) based on isotopic records of bivalves and gastropods. These authors interpreted lower SST to be the result of cool water upwelling. Brachert et al. (2014) first speculated that these isotopic studies may have underestimated water temperatures due to incorrect estimates of $\delta^{18}O_{water}$. However, based on stable isotopic records from additional coral colonies from the Florida Pennisula, Brachert et al. (2016) estimated sea surface temperatures of the Plio-Pleistocene ranged between 19.5 and 26.0 °C, agreeing that these values likely reflect periodic upwelling of cool waters peripheral to the Florida platform.

The $\delta^{13}C$ and $\delta^{18}O$ values measured in the skeleton of the *S. bournoni* specimen CCD-54102 is able to provide some additional data relevant to environmental reconstruction of the Tamiami Formation. In comparison to values from two existing $\delta^{18}O$ datasets collected from modern *Solenastrea*, the data from Pliocene sample CCD-54102 ($\delta^{18}O = -3.2‰$) is the most similar to the specimen collected from normal marine conditions along the east coast of Broward County ($\delta^{18}O = -3.3‰$) where modern SST ranges from 23 to 30 °C (Fig. 3). While exposure to freshwater precipitation will change the $\delta^{18}O$ to more negative values, exposure to evaporation or runoff of Everglades surface waters shifts values in a positive directions, similar to those seen in the modern *Solenastrea* specimen sampled from Florida Bay ($\delta^{18}O = -2.6‰$) (Swart et al., 1996). Given that the $\delta^{18}O$ value of Pliocene seawater is likely to have been similar to present day (Lisiecki and

Raymo, 2005), the Pliocene sample CCD-54102 was probably not exposed to extensive evaporation or freshwater runoff. In comparison to other Pliocene *Solenastrea* samples, the $\delta^{18}O$ values of CCD-54102 were very similar to the sample collected by Roulier and Quinn (1995) from the APAC mine of the Tamiami Formation near present day Sarasota ($\delta^{18}O = -3.2‰$). While Roulier and Quinn (1995) used data from this specimen to calculate a mean SST of 20.5–22.5 °C, we believe this to be an underestimate as a result of an improper estimate of the $\delta^{18}O_{water}$ as these authors estimated Pliocene $\delta^{18}O_{water}$ to be offset by −0.2 to −0.6‰ from a modern seawater value of 0‰. Modern seawater derived from the Gulf Stream typically has values of $\delta^{18}O_{water}$ around 1.0‰ (Schmidt et al., 1999). Furthermore, based on the compiled benthic $\delta^{18}O$ records for this period (Lisiecki and Raymo, 2005) we interpret any global ice volume effect compared to the recent to be negligible. Therefore, based on a Pliocene $\delta^{18}O_{water}$ value of 1.0‰, and the temperature equation of Roulier and Quinn (1995) we estimate a mean SST near Sarasota of 25.2 °C with an annual range of 7.8 °C and mean SST near Naples to be 25.3 °C with an annual range of 9.3 °C. These temperatures are very similar to present day mean SST at Sarasota (25.5 °C) and Naples (26.0 °C). Three other *Solenastrea* colonies sampled from the Tamiami Formation near Naples recorded significantly more positive $\delta^{18}O$ values (−2.7‰, −2.6‰, −2.6‰) suggesting the periodic influence of coastal runoff or upwelling (Brachert et al., 2016).

The $\delta^{13}C$ values of *Solenastrea* specimen CCD-54102 ($\delta^{13}C = -3.3‰$) were most similar to the modern sample from Florida Bay ($\delta^{13}C = -3.3‰$), and ~0.6‰ more negative than the modern Broward specimen ($\delta^{13}C = -2.7‰$). These more negative values could be reflecting decreased $\delta^{13}C$ values of Pliocene DIC associated with reduced water exchange across the Pliocene platform that resulted in more of the products of oxidative decay of organic material ($^{13}C$ depleted carbon, P, and N) being retained, producing platform water with a dissolved inorganic carbon content more depleted in $^{13}C$. The three *Solenastrea* colonies from the Tamiami Formation analyzed by Brachert et al. (2016) displayed significantly heavier values of $\delta^{13}C$ (−2.6‰, −2.4‰, −1.9‰), again suggesting periodic influence of coastal runoff or upwelling.

Given our similar temperature estimates near both Sarasota and Naples, the strong distinction between coral assemblages from the north and south may be reflecting either the impact of freshwater input from the middle Pliocene Bone Valley Estuary that has been mapped to the area just northeast of Tampa (Brooks, 1968), or the impact of winter cold fronts on SST in coastal embayments and nearshore environments. Sea level estimates for the MPWP range from 10 to 40 m

above present (Miller et al., 2005; Dwyer and Chandler, 2009; Dutton et al., 2015; Pollard et al., 2015), with a value of +25 m typically used in climate models (Raymo et al., 2011). With sea level 25 m higher than present, the Florida Platform south of the southern Highland Ridge would have been entirely flooded. The submerged platform separated the Loop and Florida Currents and produced conditions for strong cross platform currents analogous to present currents between the Marquesas Keys and the Dry Tortugas. These currents produced arenaceous skeletal grainstone textured limestone to the south of the Golden Gate reef trend (Meeder, 1979b) and westward migrating spits along the mainland coastline to the north (Brooks, 1968). Crossbank currents were predominately westward but may have had a seasonal component eastward. While detailed current models of a middle Pliocene submerged South Florida Platform have not been performed, we would anticipate three relevant effects that would have promoted reef development to the south: 1) increased open marine conditions in the southern portion of the Florida Platform, 2) an absence of extensive shallow bays and nearshore environments susceptible to extreme cooling during winter cold fronts, and 3) better penetration of coral propagules onto the South Florida Platform both from the predominant westward currents and enhanced eddy currents coming off the West Florida shelf.

### 5.3. Implications for Plio-Pleistocene faunal turnover

The Tamiami Formation provides a unique example of subtropical reef development during the period of Plio-Pleistocene faunal turnover (Budd, 2000; Klaus et al., 2011). The new U-Pb age date (2.99 Ma) places reef development after final closure of the Central American Seaway (CAS), which occurred between 4.25 and 3.45 Ma (Keigwin, 1982; Haug and Tiedemann, 1998; Coates et al., 2004) but prior to the initiation of extensive NHG at approximately 2.5 Ma (Raymo, 1994). This time period represents the highest Caribbean reef coral diversity of the Cenozoic (>120 species), prior to the main pulse of extinction between 2 and 1 Ma (Budd and Johnson, 1999; Budd, 2000; Klaus et al., 2011). A total of 60 species were identified from the Tamiami Formation, with extinct taxa making up between 42 and 87% of the fauna. This dominance of extinct taxa is most evident in the more northern non-reefal localities where we see *S. marylandica* and *S. crassa* clearly dominate these faunas. During the Early Miocene, *S. marylandica* could be found as far north as New Jersey (Richards and Harbison, 1942) while during the Late Pliocene it can be found as far north as the Alum Bluff Formation of the Florida Panhandle (Weisbord, 1971). The only possible occurrence of *S. marylandica* south of Florida is from the Late Pliocene Usiacuri Formation of Panama (originally described as *Septastrea matsoni*) (Vaughan, 1919). *Septastrea crassa* is known to occur as far north as the Chowan River Formation of North Carolina where it occurs as a monospecific coral thicket with an abundant mollusk fauna (Bailey and Tedesco, 1986). It is not known to occur south of Florida. Given there are no living species of *Septastrea*, the extent to which it associated with symbiotic algae is unknown. It is quite possible that *Septastrea* was either azooxanthellate (no symbiotic algae) or apozooxanthellate (intermittent symbiosis). Extinction of the two subtropical *Septastrea* species may have resulted from stronger latitudinal temperature gradients associated with the onset of NHG (Raymo, 1994). The Tamiami Formation is also characterized by a relatively high abundance of *M. hispida*. Although there is only a single other fossil locality reporting *M. hispida* outside the Tamiami Formation (Klaus et al. (2012) report four specimens of *M. hispida* from the Fish Hole Member of the Old Bank Formation (5.8–5.6 Ma) in Panama), *M. hispida* can be found living off the modern day coast of Brazil (Laborel, 1967; Leão and Ginsburg, 1997; Leão et al., 2003). Among the Brazilian coral fauna *M. hispida* has the largest spatial distribution, where it appears to have a high tolerance to cool water, high sedimentation, and fluctuating salinity. We speculate that the local

extinction of *M. hispida* in Florida was due to falling sea surface temperatures and the absence of a low latitude population from which larvae could emigrate.

Based on sea surface currents of the Caribbean and western Atlantic, the Florida Platform represents a sink population into which larvae immigrate. Thus the relatively high endemism of the Tamiami Formation (13% endemic species) could be a product of speciation resulting from limited larval supply and population connectivity. Budd and Pandolfi (2010) showed that morphologic disparity varies from the center to the edge of the Caribbean and that lineages are static at central locations but split or fuse at peripheral areas of species ranges. The five endemic taxa of the Tamiami Formation are all thought to be fairly stress tolerant (*P. sarasotana*, *O. sarasotana*, *S. dalli*, *S.* sp.A, and *S.* sp.B), and may represent stress resistant taxa that evolved during the prolonged period of west Florida reef development during the middle Pliocene. Given there was no dispersal mechanism for these taxa to emigrate back to the central Caribbean, they were prone to extinction during protracted Plio-Pleistocene cooling and deterioration of the West Florida Shelf reef environment.

Although the high-latitude Tamiami fauna is clearly unique from lower latitude Caribbean faunas (Fig. 8b), the dominant taxa of the Tamiami Formation are also dominant within many Caribbean localities. In addition to *Septastrea*, dominant taxa of the Tamiami Formation include *S. affinis*, *T. bilobata*, *P. costatus*, *M. areolata*, and *P. porites*. These branching and free-living taxa are commonly associated with siliciclastic-dominated or off-reef environments such as those found in the Cibao Basin of the northern Dominican Republic, or the Ground Creek Member of the Isla Colon Formation in Panama where reef relief is limited.

### 5.4. Is the Tamiami Formation an analog for the future?

While significant coral range expansions are already being observed in the modern oceans due to global climate change (Yamano et al., 2011; Baird et al., 2012) the potential for future coral reef range expansion is difficult to predict (Muir et al., 2015; Madin et al., 2016). The potential for latitudinal migrations will be highly dependent on local nearshore oceanographic conditions. Coral growth and reef development along the west coast of Florida is limited by extreme cold-water events associated with winter storms. While the Tamiami Formation clearly shows the potential for expanded reef development along the present day West Florida shelf, we believe significant future reef development would not be possible without a complete flooding of the South Florida Platform (>25 m) to eliminate cold water formation in shallow embayments and coastal zones.

### Competing interests

The authors declare they have no competing interests.

### Acknowledgments

### Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.gloplacha.2017.02.001.

# References

Bailey, R.H., Tedesco, S.A., 1986. Paleoecology of a Pliocene coral thicket from North Carolina: an example of temporal change in community structure and function. J. Paleontol. 60, 1159–1176.

Baird, A.H., Madin, J.S., Sommer, B., 2012. Pole-ward range expansion of Acropora spp. along the east coast of Australia. Coral Reefs 31, 1063.

Brachert, T.C., Reuter, M., Krüger, S., Lohmann, H., Petuch, E.J., Klaus, J.S., 2014. A 4.2 million years record of interglacial paleoclimate from sclerochronological data of Florida carbonate platform (Early Pliocene to recent). Global Planet. Change 120, 54–64.

Brachert, T.C., Reuter, M., Krüger, S., Kirkerowicz, J., Klaus, J.S., 2016. Upwellings mitigated Plio-Pleistocene heat stress for reef corals on the Florida platform (USA). Biogeosciences 120, 54–64.

Brooks, H.K., 1968. The Plio-Pleistocene of Florida, with special reference to the strata outcropping on the Caloosahatchee River. In: Perkins, R.D. (Ed.), Late Cenozoic Stratigraphy of Southern Florida: A Reappraisal. 2nd Annual Field Trip. Miami Geological Society, Miami, Fl, pp. 3–43.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffman, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodriques, A.S.L., 2006. Global biodiversity conservation priorities. Science 313, 58–61.

Budd, A.F., 2000. Diversity and extinction in the Cenozoic history of Caribbean reefs. Coral Reefs 19, 25–35.

Budd, A.F., McNeill, D.F., 1998. Zooxanthellate scleractinian corals of the Bowden shell bed, southeast Jamaica. In: Donovan, S.K. (Ed.), The Pliocene Bowden Shell Bed, Southeast Jamaica. Contrib Tert Quat Geol 35, pp. 47–61.

Budd, A.F., Pandolfi, J.M., 2010. Evolutionary novelty is concentrated at the edge of coral species distributions. Science 328, 1558–1561.

Budd, A.F., Johnson, K.G., 1999. Origination preceding extinction during late Cenozoic turnover of Caribbean reefs. Paleobiology 25, 188–200.

Budd, A.F., Stemann, T.A., Johnson, K.G., 1994. Stratigraphic distributions of genera and species of Neogene to Recent Caribbean reef corals. J. Paleontol. 68, 951–977.

Budd, A.F., Johnson, K.G., Stemann, T.A., 1996. Plio-Pleistocene turnover and extinctions in the Caribbean reef coral fauna. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), Evolution and Environment in Tropical America. University of Chicago Press, Chicago, pp. 168–204.

Budd, A.F., Petersen, R.A., McNeill, D.F., 1998. Stepwise faunal change during evolutionary turnover: a case study from the Neogene of Curaçao, Netherlands Antilles. PALAIOS 13, 170–188.

Budd, A.F., Johnson, K.G., Stemann, T.A., Tompkins, B.H., 1999. Pliocene to Pleistocene reef coral assemblages in the Limon Group of Costa Rica. In: Collins, L.S., Coates, A.G. (Eds.), A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama. Bull Am Paleontol 357, pp. 119–158.

Clausen, C.D., Roth, A.A., 1975. Effect of temperature and temperature adaptation on calcification rate in the hermatypic coral Pocillopora damicornis. Mar. Biol. 33, 93–100.

Colwell, R.K., 2013. Estimate S: Statistical estimation of species richness and shared species from samples. Version 9. Persistent URL <purl.oclc.org/estimates>

Coates, A.G., Collins, L.S., Aubry, M.-P., Berggren, W.A., 2004. The geology of the Darien, Panama and the late Miocene-Pliocene collision of the Panama arc with northwestern South America. Geol. Soc. Am. Bull. 116, 1327–1344.

Cooper, C., Forristall, G.Z., Joyce, T.M., 1990. Velocity and hydrographic structure of two Gulf of Mexico warm-core rings. J. Geophys. Res. 95, 1663–1679.

Cronin, T.M., 1991. Pliocene shallow water paleoceanography of the North Atlantic ocean based on marine ostracodes. Quat. Sci. Rev. 10, 175–188.

Cronin, T.M., Dowsett, H.J., 1996. Biotic and oceanographic responses to the Pliocene closing of the Central American Istmus. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), Evolution and Environment in Tropical America. University of Chicago Press, Chicago, pp. 76–104.

Denniston, R.F., Asmerom, Y., Polyak, V.Y., McNeill, D.F., Klaus, J.S., Cole, P., Budd, A.F., 2008. Caribbean chronostratigraphy refined with U-Pb dating of a Miocene coral. Geology 36, 151–154.

Dowsett, H.J., Robinson, M.M., Haywood, A.M., Hill, D.J., Dolan, A.M., Stoll, D.K., Chan, W.L., Abe-Ouchi, A., Chan-dler, M.A., Rosenbloom, N.A., Otto-Bleisner, B.L., Bragg, F.J., Lunt, D.J., Foley, K.M., Riesselman, C.R., 2012. Assessing confidence in Pliocene sea surface temperatures to evaluate predictive models. Nat. Clim. Chang. 2, 365–371.

Dutton, A., Carlson, A.E., Long, A.J., Milne, G.A., Clark, P.U., DeConto, R., Horton, B.P., Rahmstorf, S., Raymo, M.E., 2015. Sea-level rise due to polar ice-sheet mass loss during past warm periods. Science 349, aa4019.

Dwyer, G.S., Chandler, M.A., 2009. Mid-Pliocene sea level and continental ice volume based on coupled benthic Mg/Ca palaeotemperatures and oxygen isotopes. Earth Planet. Sci. Lett. 387, 157–168.

Glynn, P.W., 1973. Aspects of the ecology of coral reefs in the western Atlantic region. In: Jones, O.A., Endean, R. (Eds.), Biology and Geology of Coral Reefs, 2. Academic Press, New York, pp. 271–324.

Greenstein, B.J., Pandolfi, J.M., 2008. Escaping the heat: range shifts of reef coral taxa in coastal Western Australia. Glob. Chang. Biol. 14, 513–528.

Haug, G.H., Tiedemann, R., 1998. Effect of the formation of the Isthmus of Panama on Atlantic ocean thermohaline circulation. Nature 393, 673–676.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 1, 1–9.

Haywood, A.M., Chandler, M.A., Valdes, P.J., Salzmann, U., Lunt, D.J., Dowsett, H.J., 2009. Comparison of mid-Pliocene climate predictions produced by the HadAM3 and GCMAM3 general circulation models. Glob. Planet. Chang. 66, 208–224.

Haywood, A.M., Hill, D.J., Dolan, A.M., Otto-Bliesner, B.L., Bragg, F., Chan, W.L., Chandler, M.A., Contoux, C., Dowsett, H.J., Jost, A., Kamae, Y., Lohmann, G., Lunt, D.J., Abe-Ouchi, A., Pickering, S.J., Ramstein, G., Rosenbloom, N.A., Salzmann, U., Sohl, L.,

Stepanek, C., Ueda, H., Yan, Q., Zhang, Z., 2013. Large-scale features of Pliocene climate: results from the Pliocene model intercomparison project. Clim. Past 9, 191–209.

Hine, A.C., Halley, R.B., Locker, S.D., Jarrett, B.D., Jaap, W.C., Mallinson, D.J., Ciembronowicz, K.T., Ogden, N.B., Donahue, B.T., Naar, D.F., 2008. Coral reefs, present and past, on the West Florida Shelf and platform margin. In: Dodge, R.E., Riegl, B.M. (Eds.), Coral Reefs of the USA. Springer Science + Business Media, Berlin, Germany, pp. 127–173.

Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar. Freshw. Res. 50, 839–866.

Hoegh-Guldberg, O., Fine, M., Skirving, W., Johnstone, R., Dove, S., Strong, A., 2005. Coral bleaching following wintry weather. Limnol. Oceanogr. 50, 265–271.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nyström, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301, 929–933.

Hunter, M.E., 1968. Molluscan guide fossils in Late Miocene sediments of southern Florida. Trans. Gulf Coast Assoc. Geol. Soc. 18, 439–450.

Jaap, W.C., 2015. Stony coral (Milleporidae and Scleractinia) communities in the eastern Gulf of Mexico: a synopsis with insights from the hourglass collections. Bull. Mar. Sci. 91, 207–253.

Jones, D.S., Allmon, W., 1995. Records of upwelling, seasonality and growth in stable-isotope profiles of Pliocene mollusc shells from Florida. Lethaia 28, 61–74.

Jokiel, P.L., Coles, S.L., 1977. Effects of temperature on the mortality and growth of Hawaiian reef corals. Mar. Biol. 43, 201–208.

Keigwin, L.D., 1982. Isotopic paleoceanography of the Caribbean and east Pacific: role of Panama uplift in late Neogene time. Science 217, 350–352.

Klaus, J.S., Budd, A.F., McNeill, D.F., 2008. Assessing community change in Miocene to Pliocene coral assemblages of the northern Dominican Republic. In: Nehm, R.H., Budd, A.F. (Eds.), Evolutionary Stasis and Change in the Dominican Republic Neogene. Springer Science & Business Media B.V, Dordrecht, Netherlands, pp. 193–224.

Klaus, J.S., Lutz, B.P., McNeill, D.F., Budd, A.F., Johnson, K.G., Ishman, S.E., 2011. Rise and fall of Pliocene free-living corals in the Caribbean. Geology 39, 375–378.

Klaus, J.S., McNeill, D.F., Budd, A.F., Coates, A.G., 2012. Neogene reef coral assemblages of the Bocas del Toro archipelago, Panama: The rise of Acropora palmata. Coral Reefs 31, 191–203.

Kleypas, J.A., McManu, J.W., Mene, L.A.B., 1999. Environmental limits to coral reef development: where do we draw the line? Am. Zool. 39, 146–159.

Laborel, J., 1967. A revised list of Brazilian scleractinian corals and description of new species. Postilla 107, 1–14.

Leão, Z., Ginsburg, R.N., 1997. Living reefs surrounded by siliciclastic sediments: the Abrolhos coastal reefs, Bahia, Brazil. Proc Eighth Int. Coral Reef Symp. 2, 1767–1772.

Leão, Z., Kikuchi, R.K.P., Testa, V., 2003. Corals and coral reefs of Brazil. In: Cortes, J. (Ed.), Latin America Coral Reefs. Elsevier Science, Amsterdam, pp. 9–52.

Legendre, P., Legendre, L, 1998. Numerical ecology. Elsevier Science, Amsterdam, p. 853.

Lirman, D., Schopmeyer, S., Manzello, D., Gramer, L.J., Precht, W.F., Muller-Karger, F., Banks, K., Barnes, B., Bartels, E., Bourque, A., Byrne, J., Donahue, S., Duquesnel, J., Fisher, L., Gilliam, D., Hendee, J., Johnson, M., Maxwell, K., McDevitt, E., Monty, J., Rueda, D., Ruzicka, R., Thanner, S., 2011. Severe 2010 cold-water event caused unprecedented mortality to corals of the Florida reef tract and reversed previous survivorship patterns. PLoS One 6, e23047.

Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}$O records. Paleoceanography 20, PA1003.

Lohmann, K.C., 1988. Geochemical patterns of meteoric diagenetic systems and their application to studies of Paleokarst. In: James, N.P., Choquette, P.W. (Eds.), Paleokarst. Springer-Verlag, New York, pp. 58–80.

Lunt, D.J., Haywood, A.M., Schmidt, G.A., Salzmann, U., Valdes, P.J., Dowsett, H.J., 2010. Earth system sensitivity inferred from Pliocene modeling and data. Nat. Geosci. 3, 60–64.

Madin, J.S., Allen, A.P., Baird, A.H., Pandolfi, J.M., Sommer, B., 2016. Scope for latitudinal extension of reef corals is species specific. Front. Biogeogr. 8, e29328.

Mansfield, W.C., 1939. Notes on the Upper Tertiary and Pleistocene mollusks of peninsular Florida. Fla Geol Sur Bull. 18, 1–75.

Mayor, A.G., 1914. The effects of temperature on tropical marine animals. Carnegie I Wash. 6, 1–24.

Mayor, A.G., 1918. The lower temperature at which reef-corals lose their ability to capture food. Carnegie I Wash. 14, 212.

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

Meeder, J.F., 1979a. The Pliocene fossil reef of SW Florida. Miami Geological Society Field Trip Guide Book, p. 18.

Meeder, J.F., 1979b. The Paleoecology, Petrology and Depositional Model of the Pliocene Tamiami Formation, Southwest Florida (with Special Reference to Corals and Reef Development). (Unpublished PhD Dissertation). University of Miami, Coral Gables Florida, p. 748.

Miller, K.G., Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J., Cramer, B.S., Christie-Blick, N., Pekar, S.F., 2005. The Phanerozoic record of global sea-level change. Science 310, 1293–1298.

Milliman, J.D., 1974. Marine Carbonates. Recent Sedimentary Carbonates Part 1. Springer-Verlag, New York, Heidelberg, and Berlin, p. 375.

Missimer, T.M., 2002. Late Oligocene to Pliocene evolution of the central part of the South Florida platform: mixing of siliciclastics and carbonate sediments. Fla. Geol. Sur. Bull. 65 184 pp.

Muir, P.R., Wallace, C.C., Done, T., Aguirre, J.D., 2015. Limited scope for latitudinal extension of reef corals. Science 348, 1135–1138.

Muscatine, L., Grossman, D., Doino, J., 1991. Release of symbiotic algae by tropical sea anemones and corals after cold shock. Mar. Ecol. Prog. Ser. 77, 233–243.

Pagani, M., Liu, Z., LaRiviere, J., Ravelo, A.C., 2011. High earth-system climate sensitivity determined from Pliocene carbon dioxide concentrations. Nat. Geosci. 3, 27–30.

Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., Macardle, D., McClenahan, L., Newman, M.J.H., Paredes, G., Warner, R.R., Jackson, J.B.C., 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301, 955–958.

Pandolfi, J.M., 2015. Incorporating uncertainty in predicting the future response of coral reefs to climate. Annu. Rev. Ecol. Evol. Syst. 46, 281–303.

Pollard, D., DeConto, R.M., Alley, R.B., 2015. Potential Antarctic ice sheet retreat driven by hydrofracturing and ice cliff failure. Earth Planet. Sci. Lett. 412, 112–121.

Precht, W.F., Aronson, R.B., 2004. Climate flickers and range shifts of reef corals. Front. Ecol. Environ. 2, 307–314.

Quigley, M.C., Duffy, B., Woodhead, J., Hellstrom, J., Moody, L., Horton, T., Soares, J., Fernandes, L., 2012. U/Pb dating of a terminal Pliocene coral from the Indonesian seaway. Mar. Geol. 311–314, 57–62.

Raymo, M.E., 1994. The initiation of Northern Hemisphere glaciation. Annu. Rev. Earth Planet. Sci. 22, 353–383.

Raymo, M.E., Mitrovica, J.X., O'Leary, M.J., DeConto, R.M., Hearty, P.J., 2011. Departures from ecstasy in Pliocene sea-level records. Nat. Geosci. 4, 328–332.

Rhein, M., Rintoul, S.R., Aoki, S., Campos, E., Chambers, D., Feely, R.A., Gulev, S., Johnson, S., Josey, G.C., Kostianoy, A., Mauritzen, C., Roemmich, D., Talley, L., Wang, F., 2013. Climate change 2013: the physical science basis. In: Stocker, T.F., et al. (Eds.), The Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, United Kingdom and New York, NY, USA, p. 1535.

Richards, H.G., Harbison, A., 1942. Miocene invertebrate fauna of New Jersey. Proc. Acad. Natl. Sci. Phila. 94, 167–250.

Robinson, M.M., Dowsett, H.J., Dwyer, G.S., Lawrence, K.T., 2008. Re-evaluation of mid-Pliocene North Atlantic sea-surface temperatures. Paleoceanography 23, PA3213.

Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C., Werner, T.B., 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295, 1280–1284.

Roulier, L.M., Quinn, T.M., 1995. Seasonal- to decadal-scale climatic variability in southwest Florida during the middle Pliocene: inferences from a coralline stable isotope record. Paleoceanography 10, 429–443.

Saxby, T., Dennison, W.C., Hoegh-Guldberg, O., 2003. Photosynthetic responses of the coral *Montipora digitata* to cold temperature stress. Mar. Ecol. Prog. Ser. 248, 85–97.

Schmidt, G.A., Bigg, G.R., Rohling, E.J., 1999. Global Seawater Oxygen-18 Database - v1.21. http://data.giss.nasa.gov/o18data/.

Scholz, D., Mangini, A., 2006. Estimating the uncertainty of coral isochron U-Th ages. Quat. Geochronol. 1, 279–288.

Smith, F.G.W., 1954. Gulf of Mexico Madreporaria. In: Galtsoff, P.S. (Ed.), The Gulf of Mexico: Its Origin, Waters, and Marine Life. US Fish Wild S Fish B 55, pp. 291–295.

Swart, P.K., 2015. The geochemistry of carbonate diagenesis: the past, present and future. Sedimentology 62, 1233–1304.

Swart, P.K., Healy, G.F., Dodge, R.E., Kramer, P., Hudson, H.J., Halley, R.B., Robblee, M.B., 1996. The stable oxygen and carbon isotopic record from a coral growing in Florida Bay: a 160 year record of climatic and anthropogenic influence. Paleogeogr. Paleocl. 123, 219–237.

Takatsuki, Y., Kuragano, T., Shiga, T., Bungi, Y., Inoue, Y., Fujiwara, H., Ariyoshi, M., 2007. Long-term trends in sea surface temperature adjacent to Japan. Sokko-Jiho. 74, S33–S87.

ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). Microcomputer Power, Ithaca, NY, USA. www.canoco.com.

Vargas-Ángel, B., Thomas, J.D., Hoke, S.M., 2003. High-latitude *Acropora cervicornis* thickets off Fort Lauderdale, Florida, USA. Coral Reefs 22, 465–474.

Vaughan, T.W., 1919. Fossil corals from central America, Cuba, and Porto Rico, with an account of the American tertiary, Pleistocene, and recent coral reefs. Smith. Inst. Bull. 103, 189–524.

Weisbord, N.E., 1971. Corals from the Chipola and Jackson Bluff Formations of Florida. Fla. Bur. Geol. Geol. Bull. 53, 1–105.

Weisbord, N.E., 1974. Late Cenozoic corals of south Florida. Bull Am Paleont. 66, 259–544.

Willard, D.A., Cronin, T.M., Ishman, S.E., Litwin, R.J., 1993. Terrestrial and marine records of climatic and environmental changes during the Pliocene in subtropical Florida. Geology 21, 679–682.

Woodhead, J.D., Hellstrom, J., Maas, R., Drysdale, R., Zanchetta, G., Devine, P., Taylor, E., 2006. U-Pb geochronology of speloethems by MC-ICPMS. Quat. Geochronol. 1, 208–221.

Yamano, H., Sugihara, K., Nomura, K., 2011. Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. Geophys. Res. Lett. 38, L04601.