

Back to the future: The history of acroporid corals at the Flower Garden Banks, Gulf of Mexico, USA[☆]



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ABSTRACT

Fossil elkhorn corals, *Acropora palmata*, were discovered at the Flower Garden Banks (FGB) on the shelf-margin off the Texas coast in 2006. Radiocarbon dating revealed an *A. palmata*-dominated community aged 10,157–6838 cal BP. The *Acropora* reefs correspond in time to an interval of warmer-than-present sea-surface temperatures (SSTs) during the Holocene thermal maximum (HTM). The subsequent demise of *A. palmata* in the middle Holocene was a consequence of the inability of the shallowest reef facies to keep pace with rising sea level following complete submergence of the banks, possibly coupled with decreasing SSTs following the HTM. In 2007, the first fossil staghorn corals, *Acropora cervicornis*, were discovered at the FGB. Based on radiocarbon dating of these corals to 1027–211 cal BP, it appears that populations of *A. cervicornis* flourished in deeper waters (~25–32 m depth) on the edges of the banks until the peak of the Little Ice Age (LIA) when they died, presumably from cold-water exposure. The recent return of *A. palmata* to reefs of the FGB associated with increasing sea temperatures appears to be both an echo of the past and a harbinger of the future.

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1. Introduction

Coral assemblages on many reefs of the western Atlantic–Caribbean region have been highly volatile in recent decades. By contrast, the benthic communities at the Flower Garden Banks (FGB), two shelf-margin reefs off the coast of Texas, have been remarkably stable during this time (Aronson et al., 2005). Recent, decadal-scale stability at the FGB, however, belies centennial- to millennial-scale dynamics that are critical to understanding the history of these reefs and their future in a warming ocean.

Since the inception of long-term monitoring at the FGB in the late 1970s, the coverage of living scleractinian corals at the FGB has remained consistently in the range of ~40–60%. At the same time, coral cover has declined precipitously elsewhere in the western Atlantic (Gardner et al., 2003; Schutte et al., 2010), primarily because of a disease-induced, regional mass mortality of the ecologically and geologically dominant components of Caribbean reefs: the acroporid corals

(Aronson and Precht, 2006). The primary reason coral cover did not decline at the FGB was that the coral assemblages did not contain acroporids in the 1970s. Regional loss of the acroporids, therefore, did not affect the ecology of the FGB (Aronson et al., 2005). The recent discovery of living colonies of the elkhorn coral *Acropora palmata* at the FGB (Zimmer et al., 2006), combined with a known history of post-glacial sea-level rise in the Caribbean and GOM (Toscano and Macintyre, 2003; Törnqvist et al., 2004; Milliken et al., 2008), and published examples of latitudinal expansion of acroporid-dominated reefs during the early to middle Holocene (Precht and Aronson, 2004), led us to the hypothesis that an *Acropora*-dominated reef framework underlies and forms the foundation of the living reef community at the FGB. In this paper we report the discovery of fossil acroporid corals at the FGB and use their ages and stratigraphic positions to reconstruct the ecological history of the Banks.

2. Regional setting

The FGB are located 175 km off the coast of Texas in the northwestern Gulf of Mexico (GOM). They form part of a discontinuous arc of reefal banks along the outer margin of the continental shelf (Rezak et al., 1985). These banks are the northernmost coral reefs on the continental shelf of North America (Rezak et al., 1985). Although

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coral-dominated benthic communities exist on neighboring banks (e.g., Bright Bank, McGrail Bank, and Sonnier Bank), Blanquilla Reef north of Veracruz (980 km away) and the Alacran Reef Complex on the northern Campeche Bank (690 km away) are the nearest emergent coral reefs in the GOM (Moore, 1958; Kornicker et al., 1959; Schmahl et al., 2008). The large-scale topographic features upon which the reefs of the FGB grow were created by salt diapirs of Jurassic Louann origin (Rezak et al., 1985; Slowey et al., 2008). Understanding the connections of the FGB reefs to other reef systems in time and space is vital to managing and protecting their resources for future generations (Ritchie and Keller, 2008).

2.1. Oceanography

The main surface currents in the GOM include the Yucatan Current, the Loop Current and the Mexican Current. The Yucatan Current enters the GOM from the Caribbean through the Yucatan Channel (Fratantoni, 2001). Once in the Gulf of Mexico, the Yucatan Current initially follows the continental shelf-break from 21°N to 24.5°N and then changes to a northwesterly direction around 23.5°N, 87°W where it joins the Loop Current (Molinari and Cochrane, 1972). The Loop Current is characterized by a clockwise surface flow that extends northward into the GOM and then exits to the south via the Strait of Florida and flows into the Florida Current (Lugo-Fernández, 1998). The position of the Loop Current is variable and mesoscale, anticyclonic eddies (rings) frequently separate from, or “spin off,” the main current. These eddies drift to the west, often sitting over the FGB region for extended periods (Molinari et al., 1977; Sturges and Evans, 1983; Lugo-Fernández, 1998; Sturges and Leben, 2000; Schmahl et al., 2008). In the westernmost GOM, a western boundary current, the Mexican Current, related to wind-curl forcing (Sturges and Blaha, 1976) influences the FGB as does the Loop Current and its resultant rings (Nowlin et al., 1998; Lugo-Fernández, 2006; Deslarzes and Lugo-Fernández, 2007; Schmahl et al., 2008).

Surface wind patterns and resulting sea state are variable but show no seasonal cycle in the northern GOM (de Velasco and Winant, 1996). There is a general trend of wave propagation from ESE-to-WNW over the FGB (Rezak et al., 1985; Lugo-Fernández, 1998), correlating with both wind-vector data (de Velasco and Winant, 1996) and actual sea-surface direction and velocity measurements calculated from ships' drift records (Lugo-Fernández, 2006).

Water temperatures on the reef caps range from ~18 °C in winter to ~30 °C in late summer (Etter and Cochrane, 1975; Rezak et al., 1985; Lugo-Fernández, 1998; Precht et al., 2006). Although salinities measured at the FGB are representative of average open-ocean GOM values (Lugo-Fernández, 1998; Wagner and Slowey, 2011), persistent, westward surface-flow regimes show the presence of Mississippi–Atchafalaya River water (Salisbury et al., 2004), periodically affecting abiotic conditions on the reef caps (Deslarzes and Lugo-Fernández, 2007). Salinity in the FGB region ranges from 35–36 psu in December to 30–32 psu from late April to July (Nowlin et al., 1998). The transport of a river–seawater mix over the FGB probably explains low salinity values which are also associated with an increase in light attenuation observed as “murky, green-brown or discolored waters” over the reefs (Deslarzes and Lugo-Fernández, 2007). Otherwise, most of the time, the reef cap is bathed by clear oceanic water (McGrail et al., 1982). Tropical storms and hurricanes regularly pass within 200 km of the FGB, resulting in localized impacts on the flora and fauna (Lugo-Fernández and Gravois, 2010).

2.2. Reef communities at the Flower Garden Banks

Since the first detailed scientific observations in the 1950's our ideas regarding the reef communities of the FGB's have changed and continue to evolve (see Parker and Curray, 1956). The living reefs of the FGB comprise a deeper-water community at depths >18 m, which is presently characterized by high stony-coral cover, in the

range of 40–60%, and low macroalgal cover (Bright et al., 1984; Rezak et al., 1985; Aronson et al., 2005; Precht et al., 2006, 2008a; Hickerson et al., 2008; Schmahl et al., 2008; Johnston et al., in press). The reef surfaces are dominated by massive corals, primarily of the genera *Orbicella*, *Montastraea*, *Diploria*, and *Porites*. The present-day coral assemblages are similar to those of Bermuda, where values of coral cover can also reach or exceed 50% and the same genera of massive corals dominate the benthic community (Dodge et al., 1982; Logan, 1988; Smith et al., 2002; Creary et al., 2008). Species richness of hard corals is lower at the FGB than on most Caribbean reefs, with 21 species of scleractinians having been identified to date (Hickerson et al., 2008). The primary reason for this faunal diminution is cold-temperature limitation north of the tropical reef belt (Bright et al., 1984; Porter and Tougas, 2001).

2.3. Importance of acroporid corals

During the Late Quaternary, two coral species of the genus *Acropora* have been the most important reef-builders in the Caribbean (Goreau, 1959; Jackson, 1992; Aronson and Precht, 2001a). *A. palmata* and *A. cervicornis* were dominant space occupants of fore-reef habitats on most reefs throughout the Caribbean region (sensu lato) for thousands of years until the recent past (Aronson and Precht, 2001b). The acroporids are among the most sensitive Caribbean corals to cold-temperature stress and generally do not occur in areas where winter-time sea-surface temperatures (SSTs) drop below 18 °C (Mayer, 1914, 1915; Shinn, 1966, 2008). These areas include the reefs of Bermuda (Dodge et al., 1982; Logan, 1988; Shinn, 2008), the Florida Peninsula north of Miami (Vaughan, 1914; Jaap, 1984; Porter, 1987; Shinn et al., 1989; Precht and Aronson, 2004; Precht and Miller, 2007), the northernmost Bahamas (Lighty et al., 1980; Roberts et al., 1992; Macintyre, 2007); and the FGB (Bright et al., 1984; Rezak et al., 1985; Aronson et al., 2005). Based on presence/absence data from the northernmost portions of the Florida reef tract, it appears that *A. palmata* may be more cold-sensitive than *A. cervicornis* (Goldberg, 1973; Burns, 1985; Porter, 1987; Precht and Aronson, 2004).

In addition to temperature, other factors may be responsible for the absence of acroporid corals at the FGB. The reef caps are too deep, at >18 m, for shallow-dwelling species, especially *A. palmata*, to compete with deeper-dwelling species. Also, the remote and isolated nature of the FGB requires long-distance migration of viable larvae, limiting the recruitment potential of species such as *A. palmata* and *A. cervicornis*, which broadcast their gametes into the water column (Baums et al., 2005, 2006; Lugo-Fernández, 2006).

Aronson et al. (2005) cited three main reasons for the exceptional present-day condition of the FGB reefs: (1) the water depth of the reef caps, which buffers them from the effects of storm waves and anomalously low winter and high summer sea temperatures; (2) the remote, offshore location of the reefs, which limits human pressure and continually exposes them to clear oceanic waters; and (3) the historical absence of acroporid corals. The latter reason may seem counterintuitive, but because most of the recent change on other Caribbean reefs has consisted of the acroporids being subtracted en masse from coral assemblages (Aronson and Precht, 2001b), coral cover has remained high on reefs where massive corals dominated before and after the loss of acroporids elsewhere (cf. Precht and Miller, 2007).

2.4. Discovery of living *Acropora* at the Flower Garden Banks

The first observations of living *A. palmata* were made on the reefs of the FGB in 2003 and 2005 (Zimmer et al., 2006). These discoveries were also the deepest Caribbean records of extant *A. palmata*, at water depths down to 23 m (Fig. 1).

As previously noted, the FGB are located more than 690 km from the nearest emergent reefs dominated by *Acropora* (Jordán-Dahlgren and Rodríguez-Martínez, 2003; Schmahl et al., 2008). Ocean current models indicate that the reefs in the southern GOM are the most likely sources

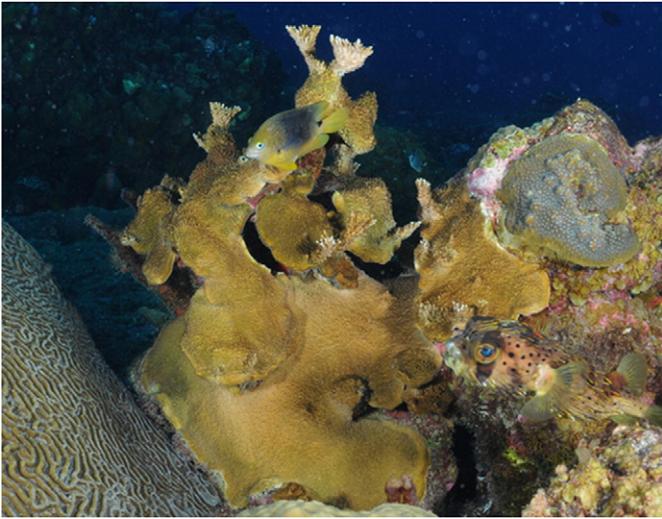


Fig. 1. Underwater photograph of recently discovered living colony of *Acropora palmata* at 23 m depth on the East Flower Garden Bank (see Zimmer et al., 2006). Photo taken by G.P. Schmahl in August, 2012.

of larval immigration to the FGB (Bright et al., 1984; Lugo-Fernández, 2006); however, larval supply from the Meso-American reef tract, Cuban reefs, and the Florida reef tract are also possible (Rezak et al., 1990; Biggs, 1992; Lugo-Fernández et al., 2001; Lugo-Fernández, 2006; Johns and Lamkin, 2008). Initial results of genetic analysis reveal that the source of the recent *A. palmata* colonies is the western Caribbean (Iliana Baums, unpublished data, 2012). No further subdivision of the western Caribbean population is apparent and thus more precise assignment to potential source locations is presently not possible (see Baums et al., 2005, 2006). Ayre and Hughes (2004) noted that the virtual absence of long-distance dispersal of corals to geographically isolated reefs renders them extremely vulnerable to various types of disturbance; however, one of the most important aspects of the discovery of living acroporid corals at the FGB is the implication that *A. palmata* larvae had to be competent for sufficiently long durations allowing them to recruit to the surfaces of the reef caps, wherever their source locations were. The same can be said for the *Orbicella annularis* species complex, which also broadcasts its gametes into the water column and is presently the dominant species at the FGB (see Szmant and Meadows, 2006). Hence, in addition to temperature, dispersal and larval duration may help explain the ranges of these corals in time and space (Davis et al., 1998; Gaylord and Gaines, 2000; Mora et al., 2003).

2.5. Post-glacial sea-level rise and reef growth

Understanding the response of reefs to sea-level rise since the last glacial maximum (LGM) is critical to deciphering the history of reef development at the FGB. At the peak of the LGM ~18 ka BP, sea level was ~120 m below present (Fairbanks, 1989; Peltier, 2002; Gehrels, 2010). As the ice caps melted and sea level rose in the latest Pleistocene, coral reefs in the tropics responded by moving poleward and expanding upslope. The accommodation space, which is space available for the reef to grow upward, increased continuously and coral populations responded, creating characteristic geometries and internal facies mosaics (Neumann and Macintyre, 1985; Schlager, 2005).

A. palmata typically lives in water depths of 5 m or less and grows rapidly (linear extension rate ~10–20 cm yr⁻¹), making it one of the most useful proxies of sea level (Gladfelter et al., 1978; Lighty et al., 1982; Toscano and Macintyre, 2003; Peltier and Fairbanks, 2006). At times, no matter how rapidly individual corals grew, the rate of sea-level rise outpaced the ability of the carbonate-sediment factory to keep up and the result was a shift, or backstepping, of the reef

facies to more shallow, shoreward positions on the shelf (Lighty et al., 1978; Hubbard et al., 1997; Macintyre, 2007; Hubbard, in press).

2.6. Range expansions during the Holocene thermal maximum

In southeastern Florida, a series of submerged, shore-parallel, fossil reef terraces reveal a precedent for the recent range expansion of *Acropora* (Precht and Aronson, 2004). This nearly continuous barrier reef system extended northward from Miami to Palm Beach County in the early to middle Holocene (Banks et al., 2007; Finkl and Andrews, 2008). The internal architectures of these reefs are replete with acroporid corals and the shore-parallel terraces represent a series of backstepped reefs (Precht et al., 2000). During the Holocene thermal maximum (HTM) (COHMAP, 1988; Ruddiman and Mix, 1991; Lin et al., 1997; Kerwin et al., 1999; Haug et al., 2001), SSTs were warmer than today in the western Atlantic, and during this period *Acropora*-dominated reefs were common along the southeastern coast of Florida (Lighty, 1977; Lighty et al., 1978; Precht and Aronson, 2004). Calibrated dates recovered from fossil *A. palmata* samples indicate that the outer reef accumulated from ~10.6–8.0 ka BP and the inner reef from ~7.8–5.6 ka BP (Toscano and Macintyre, 2003; Banks et al., 2007). These dates correspond remarkably with those proposed for the HTM (10.5 to 5.4 ka) by Haug et al. (2001). The HTM was also the period of optimum reef development for the extant Florida reef tract (Shinn et al., 1989; Lidz et al., 1997; Toscano and Lundberg, 1998).

In apparent response to climatic cooling in the late Holocene (de Menocal et al., 2000; Jessen et al., 2005), the northern limits of the *Acropora* species contracted 150 km south to Fowey Rocks (Precht and Aronson, 2004). In historical times, Fowey Rocks was the northernmost emergent reef of the Florida reef tract as well as the northernmost extent of *A. palmata* (Vaughan, 1914; Jaap, 1984; Porter, 1987; Shinn et al., 1989; ABRT 2005). Similar range expansion and contraction of a barrier reef dominated by *A. palmata* was noted off Abaco Island in the northernmost Bahamas (Lighty et al., 1980; Macintyre, 2007).

The spatial and temporal response of the *Acropora* species to climate provides a context for interpreting their past and present geographic distribution (see also White et al., 2008). The HTM also correlates with the latitudinal expansion of coral reef and mangrove ecosystems in the Pacific (Taira, 1979; Veron, 1992; Veron and Minchin, 1992; Mildenhall, 2001; Twigg and Collins, 2010; Woodroffe et al., 2010; Hongo, 2012). Evidence from both terrestrial and coastal regions shows that warming during this interval allowed many species to migrate poleward (Clarke et al., 1967; COHMAP, 1988; Salvijsen et al., 1992; Hjort et al., 1995; Dyke et al., 1996; Dahlgren et al., 2000; Carbotte et al., 2004; Jansen et al., 2009).

Although reefs at their latitudinal extremes have responded rapidly to climate flickers, results from coring and outcrop studies in the tropical Caribbean show the persistence of coral assemblages through time (Aronson and Precht, 2001a). The evidence from these *Acropora*-dominated reefs supports the notion that tropical oceanic climates have been buffered from extreme climatic variability throughout the Holocene (Macintyre et al., 1977; Fairbanks, 1989; Aronson and Precht, 1997; Gill et al., 1999; Wapnick et al., 2004; Greer et al., 2009).

3. Methods and materials

3.1. Collection/location of samples

All samples described in this report were collected by scuba diving from the East FGB, located approximately 193 km southeast of Galveston, Texas. The East FGB encompasses 67 km², sloping from its shallowest point on the reef cap at 18 m depth to the muddy seafloor at 120–140 m (Gardner et al., 1998).

3.2. Radiocarbon dating

To obtain the most accurate radiocarbon dates possible, unaltered coral samples in good taphonomic condition were chosen for analysis. The samples were air-dried, then cleaned with a steel brush to remove calcareous epibionts and submarine cements, etched with dilute hydrochloric acid, and oven-dried at 100 °C. The prepared coral samples were sent to Beta Analytic, Inc., Miami, Florida where they were radiocarbon-dated using standard techniques. Dates were calibrated to calendar years before 1950 (cal BP) after correcting for isotopic fractionation and the marine reservoir effect (Stuiver et al., 2005). The standard reservoir correction of 300–500 yr and the local reservoir correction of -36 ± 35 yr for the Gulf of Mexico (Wagner et al., 2009) were applied. In total, three samples of *A. palmata* and four samples of *A. cervicornis* obtained from the East FGB were used in the analysis.

3.3. Sea-level reconstruction

High-resolution, multibeam bathymetry was obtained from the U.S. Geological Survey (USGS) in Universal Transverse Mercator 15 N at 5-m spatial resolution, in raster grid form. Details of data correction and calibration can be found in Gardner et al. (2002). These high-resolution multibeam data have an associated error of ± 0.5 m. The ESRI ArcGIS 9.2.1 software package was used to create

and edit rasters and layers. Bathymetry data were used to generate a greyscale hillshade raster in ArcMap, using the Hillshade tool from the 3D Analyst Toolbox. The raster files were then imported into ArcScene and assigned base heights from the original bathymetry dataset to obtain 3D relief. The bathymetry raster symbology was set as a stretched color ramp and 30% transparency with the 3D hillshade raster layered underneath. A shapefile with the same coverage as the bathymetry raster was generated in ArcMap to represent water level, and a value of '0 m' was assigned to each cell. This layer was then imported into the 3D environment in ArcScene, where the base height could be adjusted as a constant value to represent various water depths, where '0 m' represented current sea level and '-35 m' represented 35 m below current sea level. Meters below current sea level and year data were obtained from Toscano and Macintyre (2003).

A grid was created as a graphic layer in ArcScene to provide reference for changing water levels. The upper boundary of the grid represents current sea level (0 m), and the lower boundary represents the deepest portion of the seafloor provided in the bathymetry dataset, 147 m depth. Values were added to the grid using the 3D Graphic Editor Toolbar. Images were exported from ArcScene as JPEGs with water level represented at 120, 60, 30 and 10 m depth (Fig. 2A–D). The bathymetric data are based on present-day conditions; however, the actual thickness of the Holocene section is unknown. Therefore, the total height of the FGB in our sea-level reconstruction through time is probably 5–10 m thicker than it actually was.

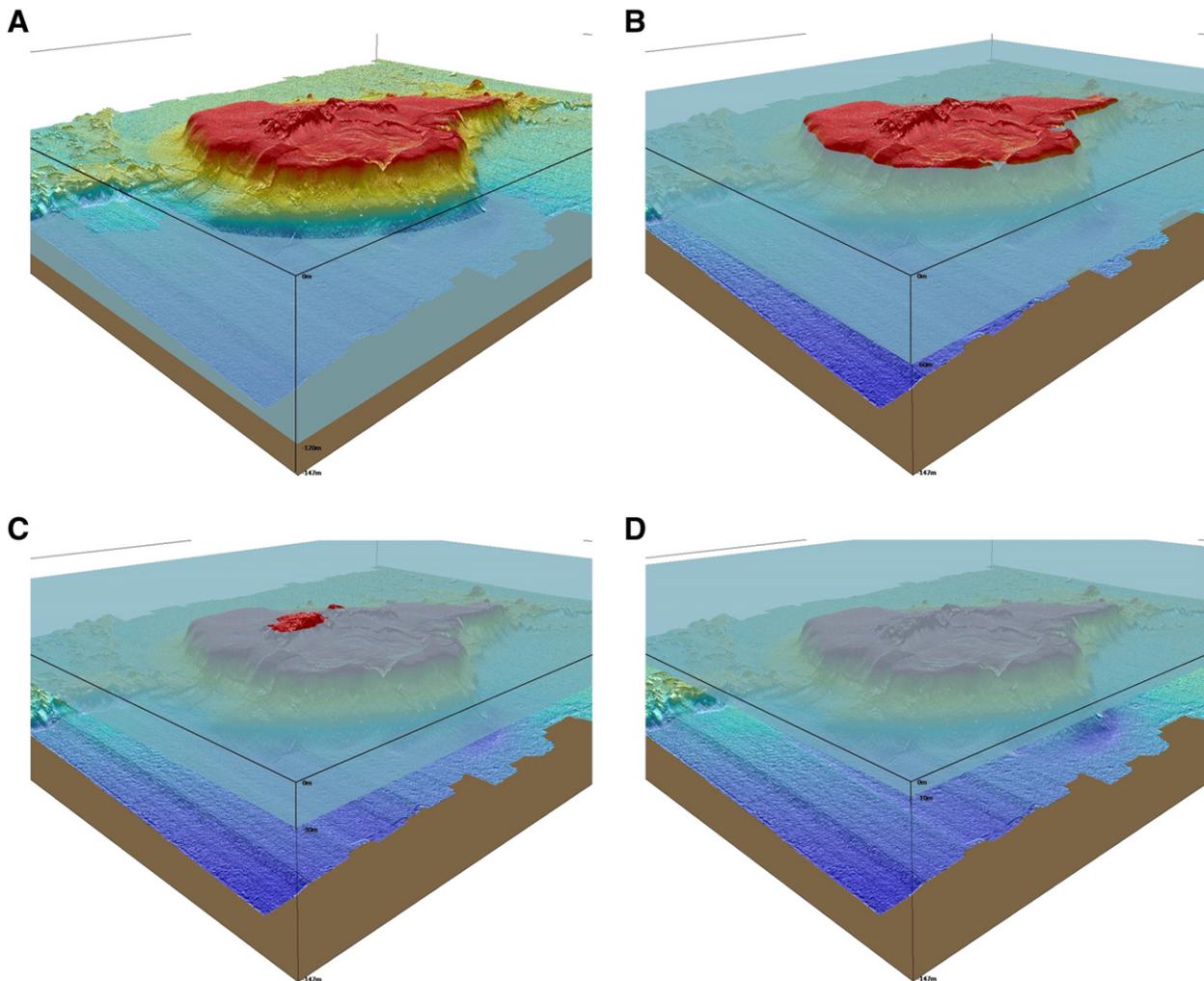


Fig. 2. Depiction of changing water levels around and eventually covering the East Flower Garden Bank associated with post-glacial sea level rise in the Gulf of Mexico. Sea level reconstruction with water depths of -120 m (A), -60 m (B), -30 m (C), and -10 m (D) graphically represented in ArcScene. Sea level data are taken from Toscano and Macintyre (2003) and superimposed on high-resolution, multibeam bathymetry obtained from the USGS (see Gardner et al., 2002).

4. Results

In June 2006, while assessing the southeast corner of the coral cap of the East FGB (27°54.49'N, 93°35.81'W), we examined an open tunnel under a series of coalesced reef buttresses that was approximately 4 m long and 2 m in diameter, which exposed in cross section a 3-m thick vertical section of the reef understory. At 21 m depth within that exposure, we found large branches and trunks (>1 m in length) of fossil *A. palmata* preserved in growth position and in good taphonomic condition (Fig. 3A). In addition, broken and transported *A. palmata* blades, also in good taphonomic condition, were admixed in the adjacent fossil reef sediment as rubble. Lewis (1984) described an almost identical arrangement of the fossil remains of *A. palmata* in the reef fabric underlying the present-day reef community in Barbados. Continued exploration of the East FGB in the summer of 2007 revealed fossil specimens of *A. palmata* under the reef cap at a number of locations in depths of 21–26 m (Fig. 3B). Taphonomically altered samples of *A. palmata* were also recovered in 2007 from the West FGB at similar depths (Zimmer et al., 2010).

In 2007, surveys along the southeast flank of the East FGB at >28 m depth revealed erosional blowout features formed by the passage of Hurricane Rita in 2005 (Hickerson et al., 2008; Precht et al., 2008b; Robbart et al., 2008). These crater-like depressions were composed primarily of rubble of the branching coral *Madracis auretenra* (= *Madracis mirabilis*; Locke et al., 2007, but see Veron, 2013) admixed with coarse-grained reef sediment. Within these features, we discovered the first colonies of branching *A. cervicornis* to

have been found at the FGB (Fig. 3C). Follow-up surveys revealed that this subsurface assemblage of fossil *A. cervicornis* was continuous over a relatively large area in water depths ranging between 26 and 32 m. Although relatively deep, these samples are still within the depth range for *A. cervicornis* from Jamaica reported by Goreau and Wells (1967). Interspersed in the field of *M. auretenra* we also found cemented thickets of fossil *A. cervicornis* exposed directly at the reef/water interface in water depths >28 m (Fig. 3D). The well-cemented branches of *A. cervicornis* were overgrown by crustose coral-line algae and covered with abundant macroalgae, primarily *Lobophora variegata*. Within these subsurface deposits we also found skeletons of the branching coral *Eusmilia fastigiata*, which were the first ever observed at the FGB (Zimmer et al., 2010). *E. fastigiata* is absent from the living community at both the FGB and Bermuda (Logan, 1988; Hickerson et al., 2008).

Radiocarbon dating of the *A. palmata* samples yielded calibrated ages of 10,157–6838 cal BP. Radiocarbon dates of the *A. cervicornis* samples revealed calibrated ages of 1027–211 cal BP (Table 1).

5. Discussion

At the peak of the LGM, sea level was ~120 m lower than today. This placed the salt-diapiric structures of the FGB at the position of the paleoshoreline (Fig. 2A; Holmes, 2011), where they towered more than 100 m above the surrounding coastal plain (see Edwards, 1971; Rezak et al., 1985). At the end of the LGM, as the glaciers melted and sea level began to rise, the bases of the FGB structures were flooded,

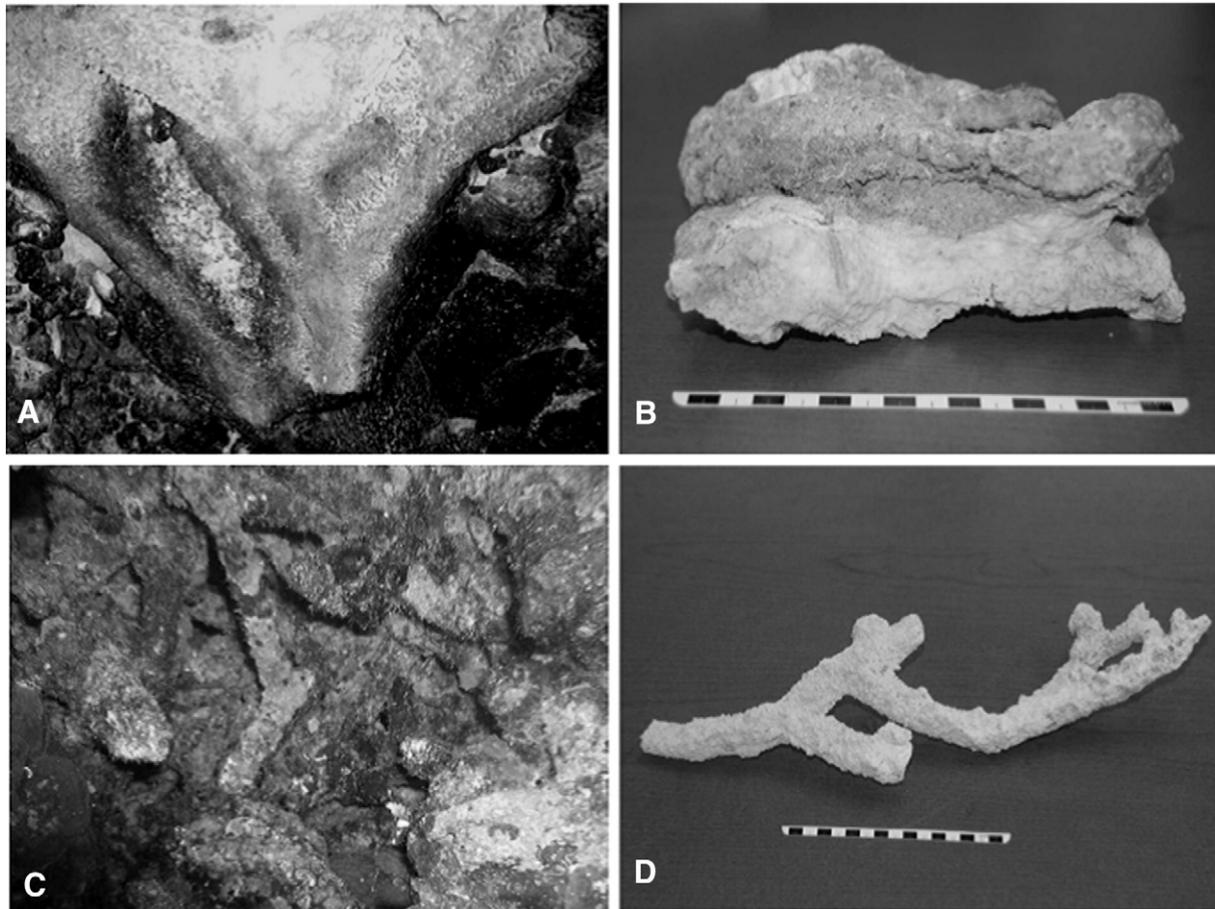


Fig. 3. Underwater photograph of sub-fossil colony of *Acropora palmata* found in growth position at –21 m on the East Flower Garden Bank (EFGB) in 2006 (A). Individual branch (blade) of *A. palmata* collected from a cave at –23 m on the EFGB in 2007. Note thick, post-mortem accumulation of epibionts, sediment, and marine cement (darker gray) covering colony (B). Underwater photograph of sub-fossil *A. cervicornis* colonies found in growth position in an open cave directly beneath the reef surface at –30 m on the EFGB. These exposed colonies were covered with living epibionts and endolithic boring sponges (C). Individual branch of *A. cervicornis* collected from erosional blowout feature at –28 m on the EFGB in 2007 (D).

Table 1
Radiocarbon dating of *Acropora* samples from the East Flower Garden Bank.

Sample #	Beta sample #	Water depth (m)	Subsea depth of sample (m)	Species	Radiocarbon age (cal yr BP)	2-sigma calibrated range (cal yr BP)
06-01	218521	21	21	Ap	6838	7014–6655
07-02	233391	26	26	Ap	10,157	10,320–9912
07-03	233392	23	23	Ap	7355	7467–7240
07-04	233393	29	30	Ac	1027	1170–903
07-05	233394	30	31	Ac	519	628–428
07-07	231801	28	29	Ac	295	436–131
07-08	231802	28	28	Ac	211	365–49

isolating them from the retreating shoreline (Fig. 2A). Sedimentary records from nearby Orca Basin revealed that from 18.0 to 13.0 ka BP, the northern GOM was dominated by detrital sedimentation as most of the meltwater from the North American continent was funneled through the southern meltwater route down the Mississippi River (Emiliani et al., 1978; Sionneau et al., 2010). During this period, the northwestern GOM was turbid, cool, and inhospitable to coral reef growth.

As the Laurentide ice sheet continued to retreat, the meltwater was diverted from its southern route to the northeast Atlantic via the Hudson River and the Saint Lawrence Seaway. Sedimentological observations from the northwestern GOM indicate that the shutdown of the southern meltwater route remained permanent after 12.7 ka BP (Montero-Serrano et al., 2009; Sionneau et al., 2010; Flower et al., 2011). Increased transport of Caribbean surface waters into the GOM region also started around this time (Sionneau et al., 2010; Flower et al., 2011). The combination of decreased influence of seasonally cold continental air masses over the northern GOM as the glacial shoreline retreated (Flower et al., 2004) coupled with meltwater discharge being diverted out of the GOM and increased input of warm, Caribbean waters into the GOM likely created conditions favorable for coral reef development (Holmes, 2011). A single sample of the coral *Siderastrea siderea*, dredged from the surface of Dream Bank on the western edge of the Texas shelf, was radiometrically dated to ~12,000 cal BP (Rezak et al., 1985; Slowey et al., 2008). Although *S. siderea* is eurytopic and can grow at temperate latitudes (Macintyre and Pilkey, 1969), the sample suggests that coral growth had initiated in the northern GOM by 12.0 ka BP. We speculate that fringing reefs began growing on the FGB at that time, especially on their eastern, windward margins. The islands that represent the FGB were now isolated on the continental shelf ~80 km from shore. They had about 33 m of relief above the waterline, with depths to the surrounding ocean floor of about 70 m (Fig. 2B).

The rate of sea-level rise was extremely rapid throughout the early phases of deglaciation. Reef growth responded by backstepping to higher, shallower positions on the banks. By 11.3 ka BP (the end of Meltwater Pulse 1B; Fairbanks, 1989), the tops of the FGB islands were about 20 m above sea level. From 10.5 to 5.0 ka BP, northward movement in the average position of the Intertropical Convergence Zone (ITCZ) had enhanced easterly winds, transporting greater quantities of Caribbean surface waters into the GOM (Hodell et al., 1991; Poore et al., 2003). Faunal-based estimates indicate that winter SSTs were as much as 2 °C warmer than modern during the middle Holocene throughout the Caribbean and GOM (Lin et al., 1997; Poore et al., 2003) with maximum warming occurring between 8 and 7 ka (LoDico et al. 2006). This interval, was optimal for the development of shallow, warm-water, reef-coral assemblages. Conditions during the HTM allowed populations of *Acropora* to emerge at the FGB. As with the Holocene reefs of southeast Florida, *A. palmata* was the dominant framework-building coral at the FGB throughout the HTM. High resolution bathymetric surveys reveal what appears to be relict, shallow-water, ESE-to-WNW trending spur-and-grove features on the bank tops (Precht et al., 2006).

By ~9.0 ka BP, the islands of the FGB were no longer exposed (Fig. 2D). These foundering banks now sat on the edge of the continental

shelf, 150 km offshore. Comparing the ages of the *A. palmata* samples from the East FGB to the sea-level curve of Toscano and Macintyre (2003) for the western Atlantic reveals that reef accumulation lagged behind rising sea level (Fig. 4). This lag placed the shallowest *A. palmata* facies in progressively deeper water. By the end of the HTM (~5.4 ka BP), the Laurentide ice sheet had completely melted. At that point, the *A. palmata* reef-crest facies was submerged at ~15 m below sea level, which was the likely maximum depth prior to drowning of these shallow-water facies. Because the crests of the banks were now submerged, there was no shallower (landward) position to which the *A. palmata* facies could backstep, and they were unable to persist in their deeper environment. The general mode of carbonate sedimentation shifted from local retention to off-bank transport (highstand shedding) lowering the vertical-growth potential of the bank top. Water quality may have also deteriorated between 7.6 – 5.2 ka due to enhanced Mississippi River discharge during the later portions of the HTM creating conditions inimical for reef growth (Tripsanas et al. 2014). Following the HTM, temperatures in the GOM cooled throughout the late Holocene in conjunction with a southward shift in the ITCZ (Hodell et al., 1991; de Menocal et al., 2000; Haug et al., 2001; Poore et al., 2003). The combination of reef submergence (i.e., incipient drowning), reduced water quality, and cooling temperatures was likely responsible for the demise of *A. palmata* at the FGB. The reefs were subsequently capped by a deeper-water assemblage dominated by massive, eurythermal corals, an assemblage that persists to this day. The deepening-upward sequence represents a 'give-up' reef (sensu Neumann and Macintyre, 1985) and has led to the progressive coalescing of the relict spur-and-grove features.

On the deeper flanks of the FGB, at >28 m depth, large fields of the delicately branched coral *M. auretenra* presently dominate the benthic community (Rezak et al., 1985), and are interspersed between ridges of plating *Orbicella* spp. corals (Precht et al., 2005). The *Madracis* fields overlie thick deposits composed of the skeletal remains of their conspecifics. Rezak et al. (1985) noted that some of these deposits also resemble large, rounded spur-and-grove features along the reef margin and may be as much as 15 m thick. Underlying the *Madracis*-dominated assemblage, we discovered extensive subsurface deposits of fossil *A. cervicornis* admixed with the *Madracis* rubble. In places, stands of fossil *A. cervicornis*, many still in growth position, were exposed at the reef-water interface. These corals yielded late-Holocene ages of 1027–211 cal BP. The older date correlates with the Medieval Warm Period (MWP), and the youngest date correspond to the peak of the Little Ice Age (LIA; Haug et al., 2001; Mann, 2002; Richey et al., 2007; Mann et al., 2009). SST records using Mg/Ca ratios provide evidence for a cooling of ~2 °C in the northern GOM at the peak of the LIA (Richey et al., 2007, 2009).

When the *A. cervicornis* initiated at the FGB is presently unknown, because the information available on the subsurface composition of the Holocene section is incomplete. What is known is that populations of *A. cervicornis* dominated the flanks of the FGB during the late Holocene, through the MWP; until they were killed by the coldest conditions of the LIA (see also Glynn et al., 1983). The fields of *A. cervicornis* were then replaced by a coral assemblage dominated by *M. auretenra*, which persists to this day. Similar replacement sequences of *M. auretenra* capping *A. cervicornis* rubble have been observed in

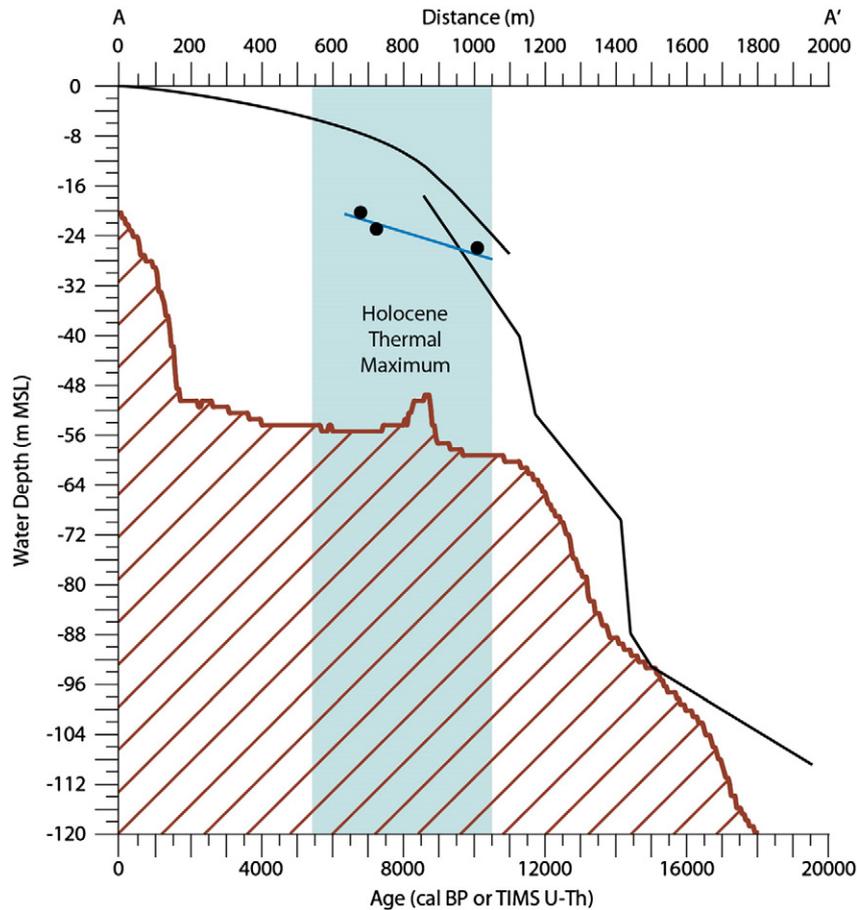


Fig. 4. Holocene sea level curve from the Caribbean (upper line) and estimated Late Pleistocene *A. palmata* sea-level curve (lower line) from Barbados data (modified from Toscano and Macintyre, 2003). *A. palmata* dates from this study (solid circles and blue line) plot below sea level and show a gradual deepening through time indicative of a “give-up” type reef. The window of the Holocene Thermal Maximum (HTM) is shown in light-blue shading (from Haug et al., 2001). Dark red line represents bathymetric cross-section A - A' across the EFGB from the reef cap at ~18 m to sediment plain at the base of the bank.

Belize and Barbados (I. G. Macintyre, personal communication, 2011). The extremely rapid growth rates of *A. cervicornis* (Macintyre et al., 1977) may also help to explain the thickness of the Holocene deposits on the flanks of the FGB previously described by Rezak et al. (1985).

The recent return of *A. palmata* colonies to the reef caps may be a bellwether of climate change (Precht and Aronson, 2004). Over the past few decades, hundreds of species have responded to recent warming trends by expanding their ranges to higher latitudes, as well as by changing their phenologies (Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003; Berge et al., 2005; Figueria and Booth, 2010; Fodrie et al., 2010; Hoegh-Guldberg and Bruno, 2010). The most parsimonious explanation for the return of *A. palmata* to the FGB is a decadal-scale increase in sea temperature (Levitus et al., 2000; Barnett et al., 2001; Hansen et al., 2006; Seidel et al., 2008), or a reduction in the frequency of extreme cold events (see Cavanaugh et al. 2013). Similar range expansions of acroporids have been observed along the east coast of Florida (Precht and Aronson, 2004; ARBT, 2005), in Australia (Marsh, 1992; Veron, 1995; Baird et al., 2012), and in Japan (Yamano et al., 2011). The discovery of living *A. palmata* at the FGB led us to predict the existence of a fossil, *Acropora*-dominated reef underlying the living reef community at the FGB. Conversely, our discovery that *A. palmata* thrived on the FGB during the warmest period of the Holocene corroborates our explanation of why this species has returned.

6. Conclusions

We propose a seven-stage chronology for reef development at the FGB during the Holocene. First, melting of the Laurentide ice sheet 18.0 to

12.7 ka BP inundated the coast and sequentially flooded the banks. Second, conditions favorable to reef development in the northwestern GOM permitted reef growth to initiate on the caps from ~12.5 to 10.5 ka BP. Third, the HTM permitted the initiation of shallow, *A. palmata*-dominated reef facies and progressive back-stepping of reef-margin facies from ~10.5 to 6.5 ka BP. Fourth, the drowning of *A. palmata* populations and loss of their associated facies at the end of the HTM led to their replacement by a ‘give-up’ facies, characterized by a deeper-water coral assemblage. Fifth, warm temperatures associated with the MWP, 1.2–0.9 ka BP allowed for the development of expansive thickets of *A. cervicornis* on the flanks of the FGB. However, when *A. cervicornis* began growing is unknown, because the information available on the subsurface composition of the FGB is incomplete. Sixth, the demise of *A. cervicornis* was associated with cold-water exposure at the peak of the LIA, ~200 yr BP. Finally, the modern, eurythermal coral assemblage is dominated by massive *Orbicella*, *Montastraea*, *Diploria*, and *Porites* on the reef cap and branching *M. auretenra* on the flanks. If the newly arrived acroporids persist and expand, we may well witness a new stage of reef development that is in reality a return to the conditions of times past.

Reefs in thermally reactive, subtropical areas are more likely than tropical reefs to change in species composition as the climate warms or cools. Specifically, the response of thermophilic *Acropora* species at the FGB to climatic changes through the Holocene provides a context for interpreting shifts in their geographic distribution. When conditions were favorable in the early to middle Holocene, acroporids dominated the shallow-reef community. When conditions deteriorated in the late Holocene, eurythermal corals rose to dominance and persisted. Comparing the structure, anatomy, and biofacies patterns in reef-building

episodes of the Holocene with the living reef community suggests that the construction of *Acropora* framework could resume in marginal environments in the near future as sea temperatures rise. These discoveries provide timely information for managers on how the threatened *Acropora* species have responded ecologically to past climatic trends. These discoveries also highlight the potential utility of using paleoecological records to outline possible future scenarios in a warming world.

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