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

William F. Precht [a,*], Kenneth J.P. Deslarzes [b,1], Emma L. Hickerson [c], George P. Schmahl [c], Marissa F. Nuttall [c], Richard B. Aronson [d]

[a] Dial Cordy & Associates, Miami, FL 33014, USA
[b] Geo-Marine, Inc., 2201 K Avenue, Plano, TX 75074, USA
[c] Flower Garden Banks National Marine Sanctuary, NOAA, 4700 Avenue U, Building 216, Galveston, TX 77551, USA
[d] Department of Biological Sciences, Florida Institute of Technology, Melbourne, FL 32901, 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.

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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* Corresponding author.
E-mail address: Bprecht@dialcordy.com (W.F. Precht).
[1] Present address: Creocean, 128 avenue de Fès, 34080 Montpellier, France.

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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 wintertime 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 *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