

MULTI-LEVEL CHARACTERIZATION OF ACROPORID CORAL POPULATIONS AT CORAL GARDENS, BELIZE: A REFUGIA IDENTIFIED

LISA GREER, Washington and Lee University

HALARD LESCINSKY, Otterbein University

KARL WIRTH, Macalester College

INTRODUCTION

At a time of dramatic worldwide coral reef decline, much of coral reef science has necessarily focused on what contributes to the demise of coral reef systems. But for reef conservation efforts to become more effective, it is increasingly important to focus on what actually makes a reef thrive. The aim of this project was to characterize the physical, biological, and ecosystem dynamics that contribute to persistence and/or resurgence of endangered acroporid coral species at Coral Gardens, to determine whether this site represents an ecological refugia in time and space, and to begin to assess whether or not marine protected status of this reef should be explored.

Acropora cervicornis (staghorn coral) and *Acropora palmata* (elkhorn coral) have been important reef builders throughout the Pleistocene and Holocene (Jackson, 1992; Hubbard et al., 1994, Greenstein et al., 1998). More recently, the hybrid *Acropora prolifera* has appeared on Caribbean reefs (Vollmer & Palumbi, 2002; Fogarty, 2007). But thriving acroporid populations are now exceptionally rare in the Caribbean and Atlantic (e.g. Precht and Aronson, 2004). The initial decline of acroporids starting in the late 1970s has been attributed to white band disease (Gladfelter 1982, Aronson and Precht 2001) which peaks with high sea surface temperatures (Randall and Woesik 2015). Since then, acroporids have been slow to recover for reasons which are virtually all tied directly or indirectly to human-induced environmental or climatic change (e.g. Jackson et al., 2001; Aronson and Precht, 2001; Precht and Aronson, 2004). Most

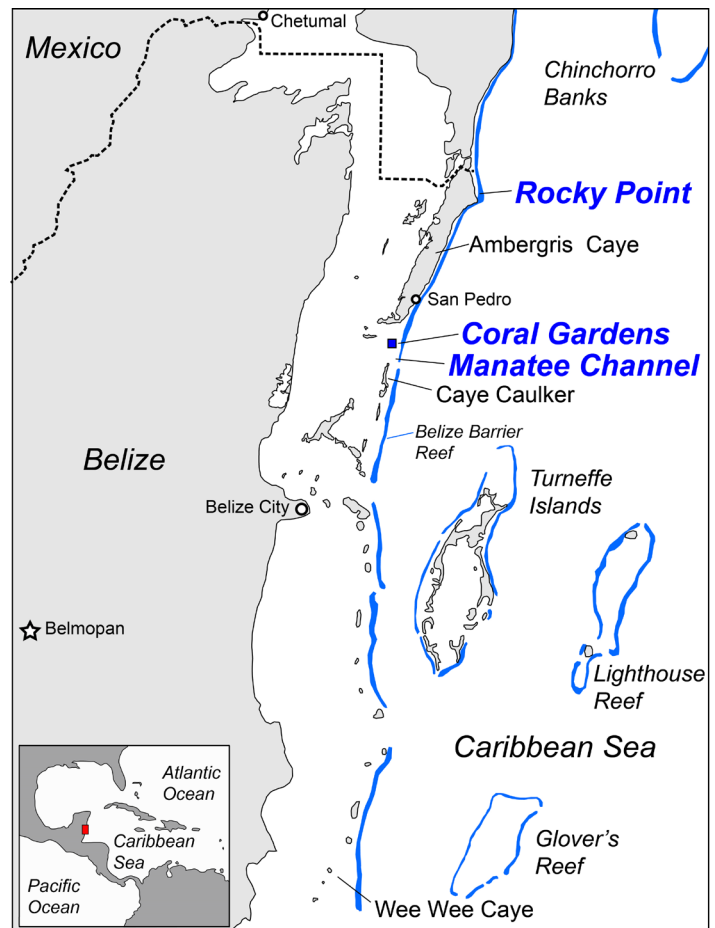


Figure 1. Location map of field sites in Belize.

living *A. cervicornis* today exist in small patches and isolated colonies, and true acroporid ‘reefs’ are now rare (Miller et al., 2009).

This project took place on the MesoAmerican Barrier Reef Complex at Coral Gardens, off southern

Ambergris Caye, Belize. Other sites included Manatee Channel between Ambergris Caye and Caye Caulker, and Rocky Point off northern Ambergris Caye (Figure 1). Coral Gardens sits between the 1,116 hectare Hol Chan Marine Reserve, created in 1987, and Caye Caulker Marine Protected Areas, but Coral Gardens has no protected status. The heart of Coral Gardens is composed of acroporid-dominated patch reefs that are variably connected to one another. In 2011 detailed observational, photographic, and field habitat surveys of Coral Gardens were established at five semi-permanent transect locations for comparison with similar data collected in 2012, 2013, and 2014 (this study). All three sibling acroporid species (*A. cervicornis*, *A. palmata*, and the hybrid *A. prolifera*) are present at these sites. Transect locations (T1-T5) are shown in Figure 2.

METHODS

This study utilized a wide variety of techniques to characterize the temporal, spatial, geochemical, geological, and ecological state of Coral Gardens. We used high resolution photo-documentation, field

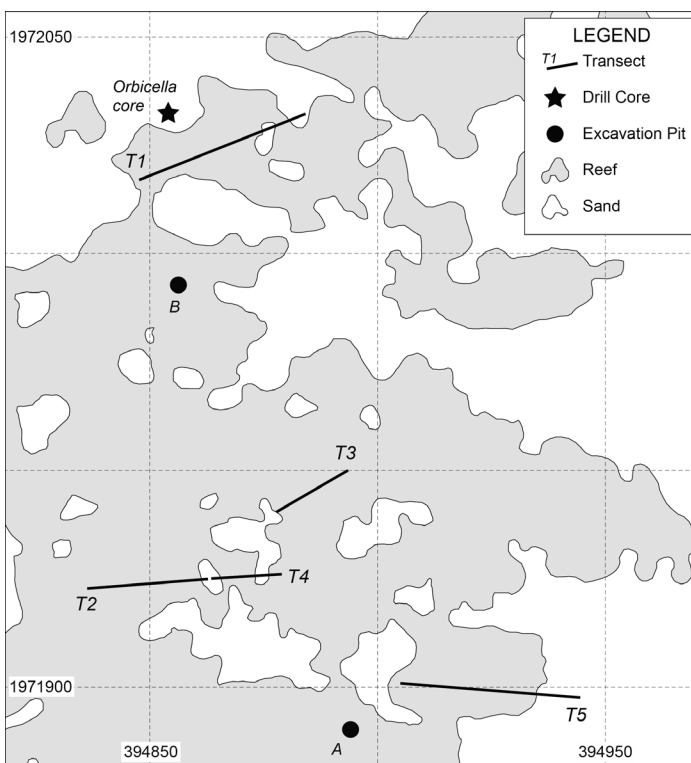


Figure 2. Map of Coral Gardens showing all 5 semi-permanent transect locations (T1-T5), the modern coral core site, and fossil coral excavation pits.

measurements, sample collection, satellite image analysis, in-situ instrumental data, genetic data, radiocarbon dating, stable isotope and elemental geochemistry, petrography, scanning electron microscopy, x-radiography, x-ray diffraction, 3D imaging, and multiple computer software programs in this work. Please see individual papers (this volume) for details.

RESEARCH

This research involved eleven students and three faculty from nine different institutions. Our combined work documented an average of 26.13% live *Acropora* coral per m² from 133 individual m² quadrats, with a low of 14.28% live coral per m² at T1 (32 quadrats) and a high of 50.27% live coral cover per m² at T5 (37 quadrats). Broadly, our work can be subdivided into five different areas of inquiry, described below.

Temporal characterization

Adele Irwin (Washington and Lee University) characterized the genetic diversity of Coral Gardens acroporids and their zooxanthellae, and found that the acroporids are not genetically diverse compared to acroporid populations in the literature. Genetic diversity is therefore not a major factor in the success of these corals in Belize. In addition, Irwin used new genetic aging techniques developed by colleagues Durante and Baums at Penn State University to estimate minimum ages of coral clones at Coral Gardens, Manatee Channel, and Rocky Point. Her genetic age estimates suggest that significant populations of *A. cervicornis* and *A. palmata* at Coral Gardens survived the 1980's Caribbean-wide collapse and that some of the 'new' hybrid *A. prolifera* clones may be at least over~100 years old. The presence of new sexual recruits in the area suggests that the acroporid patches are not strictly recruitment limited and larval transport from outside of Coral Gardens is likely.

James Busch (Washington and Lee University) focused on two separate research topics. His first goal was to determine ages of dead *A. cervicornis* from beneath the base of the reef framework (0-1.2 m depth) and underneath the living coral canopy at Coral Gardens as well as of core material from the

hardground substrate beneath the living reef. The ages are younger than expected (within the last 50-60 years) with the exception of the Pleistocene core from substrate beneath the acroporids. The dates are consistent with the corals being alive prior to the 1980s die-off, but we could not date these younger samples with high precision. These dates will form the basis for work next summer when we will sample below ~1.2 m and use complementary Uranium series ageing techniques to more precisely date the top and bottom of the Coral Gardens reef.

Spatial characterization

James Busch (Washington and Lee University) also developed, field tested, and refined a predictive GIS model capable of distinguishing live acroporid corals from other substrates using satellite imagery. Busch used the spectral signature of known acroporid patches to predict the location of previously unidentified patches. The technique distinguished acroporid-dominant coral from sandy bottom, seagrass beds, and even mixed massive coral zones. False positives and false negatives were minimized using a refined classification technique. We believe this tool is highly exportable for identifying acroporids and we will be testing its utility in Southern Belize during the upcoming 2015 field season.

Greg Mak (Trinity University) used bathymetry data, sediment analyses, stable isotope geochemistry, spatial patterns in live coral cover, and echinoderm abundance to better interpret the hydrological setting at Coral Gardens and show that hydrodynamics may be critical to the success of acroporids at this site. Mak suggests that the spatial distribution and lack of fine sediment at Coral Gardens may increase the ability of acroporids to anchor the reef on hardground substrates, particularly to the east where sediment texture and thickness indicates winnowing and transportation of sediments away from an interpreted high energy environment. Petrographic analysis of sediments and core sections shows ecologically similar environments to the modern and fossil reef. Diagenetic features and stable isotope data from core material provide evidence of subaerial exposure of the hardground that underlies the reef.

Tom Herold (College of Wooster) assessed the degree to which *A. cervicornis* may reflect or respond to dominant current patterns at Coral Gardens. Herold recorded the orientation of 8775 individual living coral branches from photographic data, plotted them using Rose diagrams, and assessed the spatial heterogeneity of branch orientation across the study site. He found that in areas of high coral cover and flatter bathymetric profile, corals exhibit stronger preferred orientation. He suggests concurrent hydrodynamic controls on both branch orientation and percent live coral at Coral Gardens. Herold shows that the dominant direction of branch orientation is into the highest velocity incoming tide. The position of Coral Gardens along a wide barrier reef cut may be promoting enhanced 'food' supply to the reef.

Carbonate budget characterization

Sarah Bender (College of Wooster) assessed the potential relationships between live coral, macroalgae, urchin densities, and scarid fish populations and she quantified the negative impact of herbivores on the carbonate budget at Coral Gardens. Her data run counter to much of the literature which often shows strong relationships between herbivores, algae, and live coral. Bender suggests that her results may be different for two important and related reasons. Our branching acroporid reefs may be functionally different from the mixed massive coral reefs that necessarily dominate the literature, and our ability to assess key reef inhabitants may be limited by our attempts at using standard methods designed for very different reef ecosystems. The intricate webbed canopy and ecosystem 'space' that acroporids provide is far more complex and 3 dimensional than Caribbean reefs that dominate today and algae or live coral cannot be assessed in a 2 dimensional photograph. Likewise, a vastly larger habitat is provided for herbivores within the acroporid reef framework, with potentially large stores of 'hidden' algae in the reef understory.

Gabriela Garcia (Oberlin College) assessed the importance of macro- and micro-borer communities in recently dead corals to the carbonate budget at Coral Gardens, with implications for interpreting the timing of death of collected samples. Garcia assigned

taphogrades as proxies for boring intensity to cross sections of coral branches and assessed the penetration rate of borers to the internal branch core. She determined that for some samples death progressed from the base to the tip of the coral which is consistent with the tissue die-off during White Band Disease, and not predation. Garcia discusses the potential links between mortality of individual branches and El Niño occurrences in Belize. She also shows that highly bored branches often still have a high degree of structural integrity which may be a function of the competing action of encrusters on the reef.

Erin Peeling (Penn State University) assessed the spatial heterogeneity of live coral abundance across Coral Gardens transects using quadrat-specific photographic data. By comparing overlapping photographs of individual branches from 2012-2014 she was able to quantify the linear extension rate and carbonate production by *A. cervicornis* at this site. She also tested whether carbonate budget procedures developed primarily for massive corals were applicable to branching coral reefs. Peeling concluded that % cover data for *A. cervicornis* gave an erroneously high result and that counts of active growing tips provide a far more accurate estimate of carbonate production. Together with Bender, Martin, and Garcia, her study shows that Coral Gardens is currently in a constructional rather than a destructional growth phase. She created a forward model that can test Coral Gardens growth under decreased linear extension rate or live coral due to environmental impacts.

Ecological systems characterization

Shannon Dillon (Colgate University) focused on the hybrid *A. prolifera* and addressed the question of whether it can be distinguished from parent species or identified in the fossil record. It has been suggested that *A. prolifera* is a new hybrid that may even be overtaking the functional role of its parent species on some Caribbean reefs. Yet the timing of hybridization is unclear. While *A. prolifera* has not been identified in the fossil record, data from Irwin (this volume) suggests that *A. prolifera* may not be new to Coral Gardens. Dillon provides a detailed morphometric and taphonomic analysis of all three acroporid siblings and investigates the preservation potential and

identification characteristics of the hybrid species. She suggests that *A. prolifera* is unique enough from its parents to be identified in the fossil record and that its intermediate preservation potential should not inhibit it from being found if it existed prior to modern times. The fossil record should be reexamined to see if *A. prolifera* has been overlooked.

Zebulon Martin (Otterbein University) investigated the potential role of *Stegastes planifrons*, (threespot damselfish) in promoting or inhibiting acroporid growth at Coral Gardens. The literature suggests both positive and negative impacts of damselfish on acroporid growth via a variety of mechanisms. It has even been suggested that damselfish may be a keystone species for acroporid reefs. Martin documented a positive correlation between damselfish and their urchin competitors, suggesting that herbivory on acroporid reefs is not as limited or competitive as on mixed massive coral zones that dominate the Caribbean today. He found few damselfish feeding scars and that damselfish abundance was positively correlated with coral structure. These findings suggest that the fish-coral relationship may be driven more by the coral than the damselfish, and therefore damselfish should not be considered a keystone species.

Geochemical characterization

Ilian DeCorte (Macalester College) used density banding and annual linear extension rates from x-radiography and stable isotope geochemistry of coral cores, as well as in situ temperature and salinity measurements to characterize environmental conditions at Coral Gardens and Rocky Point. He found that while the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signatures at Coral Gardens and Rocky Point are similar, the stress histories recorded in the coral density bands are not. He also documented a possible long-term decline in linear extension rate at Coral Gardens which is consistent with sclerochronology records elsewhere. It has been suggested that these declines are a function of global climate and environmental change.

Sarah Holmes (Beloit College) investigated the potential for obtaining high resolution paleoenvironmental data using geochemical data from branching acroporids. Branching corals are rarely used as archives of marine conditions, as their skeletal

morphology and lack of clear annual density bands makes them difficult to utilize. Holmes compared stable isotope data from three different sampling methods to assess the utility of each. She discovered, that low-resolution sampling methods potentially capture longer-term reef conditions through time. She also discovered that while high resolution sampling strategies appear to recover sub-annual environmental change, transverse and longitudinal sampling values may reflect different fractionation effects between axial growth (extension) and transverse outer growth (thickening). Therefore different sampling strategies have potential to resolve different questions. Holmes points out that the high growth rate of *A. cervicornis* might also complicate paleoenvironmental interpretations.

IMPLICATIONS OF THIS WORK

Is Coral Gardens a refugia?

This project was designed to characterize the extent, health, and contributing factors to the success of acroporid populations at Coral Gardens, Belize against a backdrop of global decline of these endangered corals. Our work suggests that Coral Gardens is a true ecological refugia for acroporids, and particularly for *A. cervicornis*. Genetic aging data from Irwin show that at least some acroporid populations survived the Caribbean-wide collapse of acroporids that began in the 1980's but also that Coral Gardens has served as a site for new acroporid recruitment. The extent of acroporid colonization is shown by our mapping of the patches at Coral Gardens by Busch and by our reconnaissance of other patches nearby and to the north at Rocky Point.

Should Coral Gardens be protected?

Our data show that Coral Gardens is functionally different than the vast majority of surviving reefs today. In this volume data from Busch shows that Coral Gardens is relatively unique in the abundance of acroporids with respect to the literature. Martin and Bender show that the relationships between herbivores, damselfish, algae, and live coral are not the same as for well-studied mixed massive coral reefs that remain today. The combined work of Peeling, Bender, and Martin show that this reef is in a

constructional phase despite unusually high bioeroder abundance. Garcia and Herold show that acroporids at Coral Gardens appear to maintain a high degree of structural integrity despite currents and micro- or macro-boring intensity. Data from Mak and Herold suggest that hydrodynamics may play a key role in acroporid abundance at Coral Gardens.

We suggest that Coral Gardens may benefit from conservation efforts and that Marine Protected status should be considered for this site. We have not attempted to merge our scientific findings with the very important sociological, political, and economic issues that MPA status would have to consider. We also understand that MPA status does not always effectively protect coral health, particularly against global or regional climate or environmental change. But our data show that Coral Gardens is unique in the abundance of acroporids. Irwin also shows that these coral populations are not genetically diverse which may increase vulnerability to unforeseen future events. DeCorte documents environmental stress events and an overall trend in decreasing linear extension rate encoded in coral skeletons and Garcia shows that White Band Disease may be responsible for some coral mortality at this site.

Future Work

This study, and the data presented in this volume provide rich opportunities for the continued study of Coral Gardens, and acroporid corals in general. While data from Irwin suggest that some of the hybrid *A. prolifera* may predate reports in the literature, Dillon shows that *A. prolifera* preservation potential is high and provides the tools to recognize this species in the fossil record in the future. Holmes provides valuable data and guidance for acroporid sampling strategies for future retrieval of paleoclimate information from the past. Mak and Herold provide the scientific rationale for a detailed hydrodynamic study of Coral Gardens.

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