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Environmental Factors Controlling Community Structure, Morphology and Linear Extension of Mid-Holocene Reef Corals from Cañada Honda, Southwestern, Dominican Republic

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Abstract. The Cañada Honda (CH) fossil coral reef, located in SW Dominican Republic, provides a unique opportunity to examine reef accretion in a high-sedimentation environment between 9.0-5.0 ky ago. Annual linear extension of fossil corals was determined for comparison with data from modern coral reefs. The reef is characterized by the high abundance of sediment-tolerant coral species, their tendency to form almost monospecific stands and grow as domes-cones with ragged margins. Also, colonies of *Montastraea faveolata* commonly contain bands of sediment incorporated within their skeletons. Calibrated radiocarbon ages of fossil corals range from 9,256±137 to 6,737±94.5 BP. Correlation with Holocene sea-level curves indicates that most corals on CH developed at depths greater than 15m. Growth rates varied from 0.09-0.44 cm/yr and suggest reduced light penetration caused by coral growth at such depths. Reef sediment is characterized by more than 85% carbonate material. A significant portion of the carbonate is allochtonous and was derived from nearby Neogene limestones. The reef was able to survive under these conditions because of the high carbonate content of incoming terrigenous sediment and that storms probably occurred sporadically providing intervening low-sedimentation periods during which reef corals could respond and grow back, "keeping-up" with sedimentation.

Key words: Holocene, siltation, linear extension, Caribbean

Introduction

Measurements of coral growth rates (as vertical extension) are used regularly as reef health indicators particularly in environments characterized by high terrigenous sediment input (e.g. Cortés and Risk 1985). Turbidity associated with suspended sediment and enhanced phytoplankton productivity reduces light penetration and the photosynthetic yield in corals (Cortés and Risk 1985; Philipp and Fabricius 2003) while the removal of settled particles from the coral increases metabolic costs (Telesnicki and Goldberg 1995; Fabricius 2005). As a result, a decrease in the annual growth rates of corals is expected.

For the past three decades a decline in reef coral abundance and diversity is being observed globally (Hughes 1994; Ginsburg 1994; Aronson et al. 2002) due to anthropogenic and natural causes. Increased coastal development and agriculture runoff leading to higher sediment accumulation and resuspension, together with discharge of sewage and industrial waste into the ocean have been blamed as major causes for modern coral reef decline (Hughes 1994; Hughes and Connell 1999; Morelock et al. 2001). A major question exists in terms of the relative roles that anthropogenic and natural disturbances play in the current trend of reef decline. The majority of the studies concerning reef health, siltation stress and low coral growth rates come from modern reef sites, many of them affected to a great extent by anthropogenic disturbance (e.g. Cortés and Risk 1985; Scoffin 1986; Edinger et al. 1998, 2000). Therefore it can be very difficult to differentiate the individual effects of natural versus anthropogenic disturbance. Some studies on coral reefs with natural high sediment input and resuspension show noteworthy differences compared with those with significant anthropogenic disturbance (Larcombe et al. 2001).

A reasonable way to differentiate anthropogenic disturbance versus natural disturbance is to study records of well-preserved fossil reefs in detail and compare the data with that gathered from modern coral reefs. This kind of approach has already been implemented in several studies (e.g. Pandolfi and Jackson 2001; Aronson et al. 1998; 2002), leading to the conclusions that current coral degradation has no precedent in the recent past. The purpose of this paper is to present data on fossil coral growth rates from the

Mid-Holocene Cañada Honda (CH) fossil coral reef of southwestern Dominican Republic (Fig. 1). The data presented is part of a larger study in which the main interest is to elucidate the pattern of reef development within natural conditions of high sedimentation and make comparisons with information gathered in modern reef environments under similar conditions. The CH fossil reef provides exceptional advantages that make it suitable for this kind of study. It displays remarkably well-preserved subaerial exposures of shallow-water reef environments dated between 10,000 to 4,500 years ago (Taylor et al. 1985). The young age (Mid Holocene) and the relatively dry climate has resulted in excellent preservation of original aragonitic skeletal mineralogy of fossil corals (Greer 2001). The CH fossil reef thrived in a high sediment environment as pointed out by Mann et al. (1984), Taylor et al. (1985) and Stemann and Johnson (1992) providing a unique opportunity for comparing a reef that developed under conditions of natural stress and disturbance with modern reefs that have been subjected to varying degrees of anthropogenic stress.

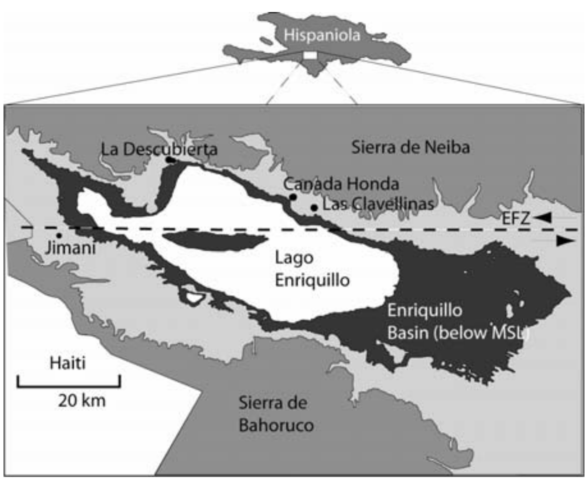

Figure 1: Map of the Enriquillo Lake area showing location of the Cañada Honda fossil reef. Black-colored areas represent land below present sea level. Dashed line represents location of the Enriquillo Fault Zone (EFZ).

Material and Methods

Field data collection

Variations in the sedimentary environments as well as coral assemblages were studied using quadrats along 18 vertical transects (Fig. 2) for a total of 67 quadrats. Information such as presence, abundance, morphology and distribution of corals were determined as well as the presence of other important taxa such as gastropods, serpulids, oysters and echinoderms. The importance or presence of reef sediment within the quadrat was also measured. Quadrats were placed on vertical exposures and each of the 100 points was counted as sediment or fossil. Locations for vertical transects were randomly selected and an effort was made not to bias placement on especially large or well preserved colonies.

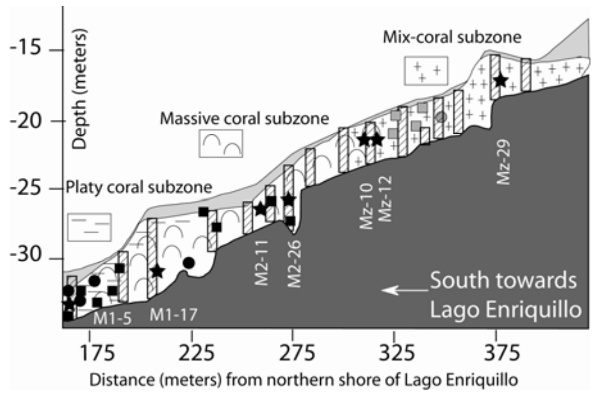

Figure 2: Cross-section of the Cañada Honda fossil reef showing location of transects (bars) and corals sampled for growth rate analyses. Squares represent *M. faveolata* samples and circles represent *S. siderea* samples. Difference in color denotes different subzones. Star represents samples for radiocarbon dates. *Acropora cervicornis* zone not shown.

Coral Growth Rates

Growth rate analyses focused on the corals *Montastraea faveolata* and *Siderastrea siderea* which are the two most abundant massive coral species in the CH fossil reef and additional growth rate data are available for each (e.g. Cortés and Risk 1985; Gischler and Oshmann 2005). Samples were collected randomly, identified and all the pertinent field information (photography, elevation, location in the reef) recorded (Fig. 2). To determine growth rates, corals were cut into 3-5 mm wide slices. The central slab of the colony, where the maximum growth occurs, was then polished and X-radiographed to reveal skeletal growth patterns. The radiographs were then scanned and the high and low density growth bands revealed by X-rays were measured using Coral XDS v. 3.0 (Coral X-radiograph Densitometry System) software that detects and measures changes in image density.

Radiocarbon dates

Seven of the coral specimens analyzed for growth rates were chosen for radiocarbon dating. The samples were selected according to their location on the CH reef in order to obtain coral ages at different elevations throughout the outcrop. In conjunction with well established Holocene sea-level curves (e.g., Toscano and Macintyre, 2003), radiocarbon ages were used to constrain paleodepths of the corals at their time of growth as well as determine the pattern of reef accretion through time. Radiocarbon analyses were conducted at the National Ocean Sciences AMS Facility of the Woods Hole Oceanographic Institution in Massachusetts, USA. Radiocarbon ages obtained from the AMS facility were then calibrated to account for the ^{14}C local marine reservoir. Calibration was done using the CALIB software v. 5.1.

Sediment sampling and analyses

Nineteen sediment samples from the CH fossil reef were analyzed for this study. In addition, four sediment samples from a fluvio-deltaic sequence overlying the Mid-Holocene fossil coral reef from Las Clavellinas (Fig. 1) were analyzed for the purpose of determining composition of allochtonous terrigenous sediment that reached the former Enriquillo Bay. Analyses consisted of determination of the relative organic and carbonate content. A portion of each sample was weighed and then Clorox was added to remove organic matter. Samples were washed with distilled water, dried in an oven at 100˚C and weighed again to determine the percent of organic matter removed by the Clorox. This process was repeated again with a solution of 10% Hydrochloric Acid (HCl) to remove the $CaCO_3$ of the samples.

Results

Community structure

Twenty-two Scleractinian coral species were identified in the CH fossil reef (Table 1). The most abundant coral species is the massive coral *Siderastrea siderea* with approximately 47.4% of the coral counts followed by *Montastraea faveolata* (8.73%), *Undaria (Agaricia) agaricites* (7.66%), *Colpophyllia natans* (5.83%), *Montrastraea franksi* (4.13%), and *Acropora cervicornis* (3.86%). In general, the CH fossil reef can be divided into two major zones. The first, a branching or *Acropora cervicornis* zone which dominates throughout the upper reef (~0 to -15 m elev.). In this zone, the coral species *Acropora cervicornis* has an abundance of 37.9% followed by *Montastraea annularis* and *Undaria (Agaricia) tenuifolia*. The second zone or *Siderastrea siderea* zone consists mostly of massive corals where the coral species *Siderastrea siderea* range from 50% to 70% and can be divided into the following three subzones in descending elevation order (-15 to -35 m elev.); a high diversity assemblage or mix-coral subzone, a low diversity assemblage or massive coral subzone and a platy coral subzone (Fig. 2). A similar pattern of coral species distribution was obtained by Stemann and Johnson (1992).

Coral morphologies were grouped into five categories. These are platy, hemispherical, conical, columnar, and branching (Table 2). The dominant morphology in the CH fossil reef is hemispherical (34.9%), followed by conical (20.5%), branching (16.8%), platy (16.4%) and columnar(11.4%). Most of these morphologies are associated with reduced light penetration and turbidity caused by high sedimentation (James and Bourque 1992; Van Woesik and Done 1997). In addition, 51% of the counts from the massive coral morphologies (i.e. hemispheres, columns and cones) have ragged margins (Table 2) which is indicative of sedimentation rates equal or almost equal to the coral growth rates (James and Bourque 1992).

Coral Growth Rates

Twenty-five coral colonies were analyzed to determine annual growth rate. For the massive coral *Montastraea faveolata*, annual growth rates ranged from 0.09 to 0.44 cm/yr (Table 3). In coral colonies of *Siderastrea siderea*, annual growth rate varied from 0.2 to 0.4 cm/yr. Compared with *Montastraea faveolata*, *Siderastrea siderea* showed less variability in the annual growth rate values (Table 3).

Table 1. Distribution (% counts) of coral species and sediment in Cañada Honda

Coral species	**C. Honda**
Siderastrea siderea	47.38
Montastraea faveolata	8.73
Stephanocoenia intersepts	1.25
Madracis spp.	0.84
Dichocoenia stokesi	1.33
Colpophyllia natans	5.83
Agaricia lamarcki	2.05
Undaria agaricites	7.66
Acropora cervicornis	3.86
Oculina diffusa	0.41
Porites porites	3.86
Siderastrea radians	0.45
Helioceris cucullata	0.74
Mussa angulosa	0.14
Manicinia aerolata	0.23
Eusmilia fastigiana	3.18
Montastraea annularis	1.97
Montastraea franksi	4.13
Montastraea cavernosa	2.34
Porites astreoides	0.33
Undaria tenuifolia	1.46
Scolymia spp.	0.02
Other ‡	1.81
Sediment	22.62†

*out of 4871 coral counts

‡ Refers to unrecognizable, highly damaged coral colonies

†out of 6295 which is the total number of counts

Table 2. Summary of coral morphology distribution along Cañada Honda (% counts)

Morphology	**Smooth**	**Ragged**	**Total %**
Branching	16.8	-	16.8
Platy	16.4	-	16.4
Cones	10.5	10.0	20.5
Columns	8.6	2.8	11.4
Domes	13.7	21.2	34.9

Radiocarbon ages

Calibrated radiocarbon ages obtained from the seven CH coral samples ranged from 9,256.0±137 BP to

6,736.5±94.5 BP (Table 4). The oldest age is from a specimen of *Montastraea faveolata* (9,256.0±137 BP) followed by a specimen of *Siderastrea siderea* (8,628.0±165 BP). The youngest age was found in a specimen of *Montastraea faveolata* (6,736.5±94.5 BP) followed by a specimen of *Siderastrea siderea* (7,465.0±83 BP). Correlation of radiocarbon ages with a well-established Holocene sea-level curve (i.e. Toscano and Macintyre, 2003) helps establish the approximate paleodepth at which coral specimens grew. Except for coral sample Mz-29, which occurred in a topographic high (Fig. 2), the remaining corals developed at paleodepths of no less than 15m (Table 4).

Table 3. Results of measurements of coral growth rates from Cañada Honda

Coral sample	N	Mean annual extension (cm/yr)	Error (2σ)
Montastraea faveolata			
Pz-01	31	0.340	0.042
M1-5	28	0.091	0.013
M1-10	35	0.280	0.037
M1-13	31	0.248	0.019
M1-30	27	0.286	0.004
M2-6	22	0.363	0.024
M2-10	31	0.175	0.017
M2-11	107	0.142	0.014
M2-17	19	0.313	0.045
M2-21	12	0.278	0.062
M3-8	35	0.189	0.032
M3-18	21	0.299	0.055
M3-20	16	0.213	0.053
Mz-10	8	0.351	0.079
Mz-14	15	0.305	0.049
Mz-16	15	0.410	0.035
Mz-29	17	0.437	0.042
Siderastrea siderea			
M1-17	15	0.382	0.042
M1-22	17	0.269	0.033
M2-1	42	0.256	0.020
M2-2	8	0.400	0.092
M2-26	16	0.304	0.036
Mz-12	43	0.335	0.024
Mz-21	9	0.246	0.034
Pz-02	24	0.222	0.031

Sediment composition

Sediment composition analyses conducted on the nineteen sediment samples from the CH fossil reef are characterized by a high percentage of carbonate (i.e. $CaCO_3$) material (Table 5). Carbonate content varied from 84% to 96%. In contrast, the sediment samples from the fluvio-deltaic deposits in Las Clavellinas are characterized by carbonate content varying from 41% to 69% (Table 5).

Discussion and Conclusions

The Mid-Holocene Cañada Honda fossil reef in the Dominican Republic shows signs of development in an environment of high sedimentation based on the relatively high abundance of sediment-tolerant coral species, the tendency of these to form almost monospecific stands, and the propensity of individual colonies to grow as encrusting, dome-shaped, platy-like forms. Also the finding of sediment incorporated into coral skeletons supports the idea of siltation stress during the accretion of the reef.

Coral growth rates measured for fossil *Montastraea faveolata* in CH are relatively low compared with growth rates of modern corals from sites throughout the Caribbean. These low growth rates resulted from low light penetration most likely from growth at 15m or more (Table 4). Nonetheless, if these conditions are correct, coral development occurred at depths not expected for a reef under siltation stress. However, the high carbonate content of the incoming terrigenous sediment allowed greater light penetration than similar amounts of siliciclastic sediment, and,

Table 4. Summary of calibrated radiocarbon ages from coral samples in Cañada Honda

Coral sample	Cal. ^{14}C ages (BP)	Error (2σ)	Paleodepth (±1m)
Mont. faveolata			
M1-5	9,256.0	137	16.0 m
M2-11	7,882.5	99.5	18.0 m
Mz-10	6,736.5	94.5	16.0 m
Mz-29	7,705.0	106	8.0 m
Sid. siderea			
M1-17	8,628.0	165	18.0 m
M2-26	7,846.0	97	16.0 m
Mz-12	7,465.0	83	15.0 m

Table 5. Results of sediment composition analyses from Cañada Honda reef sediment and Las Clavellinas fluvial sediment (LCS samples)

Sediment sample	% Organic Matter	% $CaCO_3$	% Non-Carbonate
LCS-1	3	69	28
LCS-2	2	50	48
LCS-3	5	41	54
LCS-4	8	54	38
S-43-1	2	89	9
S-43-2	4	88	8
S-43-3	4	92	4
S-67-1	4	92	4
S-67-2	0	96	4
S-67-3	5	86	9
S-104-1	0	93	7
S-104-2	3	94	3
S-104-3	12	84	4
S-104-4	5	88	7
S-136-1	3	94	3
S-136-2	2	90	8
S-176-1	8	90	2
S-176-2	3	94	3
S-176-3	7	90	3
S-232-1	2	94	4
S-232-2	3	96	1
S-232-3	4	95	1
S-400-1	2	95	3

thus, allowed corals to grow at greater depths than typically expected under these conditions. Other possibilities are that even though sedimentation was high, it occurred sporadically allowing time for the reef corals to respond and grow back, in such a way that they were able to "keep-up" with sedimentation and sea-level rise.

The coral growth rates measured for *Siderastrea siderea* in CH are similar to growth rates of this coral from other sites in the Caribbean including sites in shallow water, with siltation stress and great depths. Also, *S. siderea* colonies from CH did not show clear bands of incorporated sediment into the skeleton compared with those of *Montastraea faveolata*. This fact highlights the ability of this coral to reject sediment and survive in stressful environments. Therefore, coral growth rates of *Siderastrea siderea* should not be taken as an unequivocal indicator of turbidity or other signs of reduced light penetration until more is known about the feeding mechanism, metabolism and skeletogenesis of this coral species.

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