

How vulnerable is *Acropora cervicornis* to environmental change?

Lessons from the early to middle Holocene

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ABSTRACT

The coral *Acropora cervicornis* is considered a modern environmental indicator species, vulnerable to anthropogenic stress and rapidly disappearing throughout the Caribbean. Causes for its decline have been attributed to both natural and anthropogenic factors. Physical and geochemical data are used to explore conditions under which this species thrived in early to middle Holocene reef deposits (ca. 9.4–5.4 ka) of the Enriquillo Valley, southwestern Dominican Republic. This study shows that *A. cervicornis* flourished during a 4000 yr period spanning the Holocene Thermal Maximum, and high-resolution radiocarbon dating reveals continuous growth for at least 2000 yr. Holocene *A. cervicornis* survived large-scale climate and environmental changes that included high temperatures, variable salinity, hurricanes, and rapid sea-level rise with remarkable resilience. Our data suggest that the recent decline in *A. cervicornis* is anomalous and likely tied to ecosystem change beyond natural causes.

INTRODUCTION

Corals have been referred to as the “canaries in the coal mine” of our seas, with widespread decline in coral reefs (e.g., Gardner et al., 2003; Pandolfi et al., 2005) signaling poor ocean health. *Acropora* spp. corals may be particularly sensitive to environmental change (Precht and Aronson, 2004; Greenstein and Pandolfi, 2008). A dominant Caribbean reef builder in the Pleistocene and Holocene (Jackson, 1992; Hubbard et al., 1994), *Acropora cervicornis* (staghorn coral) has suffered a dramatic decline over the past three to four decades (e.g., Aronson and Precht, 2001). In 2007 the U.S. Department of the Interior added *A. cervicornis* to the Endangered and Threatened Wildlife list. Proposed causes for the decline of *A. cervicornis* and other corals include stress induced by changes in temperature, eutrophication, herbivory, disease, storm activity, salinity, sedimentation, and other anthropogenic activity (e.g., Hoegh-Guldberg, 1999; Jackson, 2001; Wapnick et al., 2004). Possibilities for recovery of high-resolution data on early to middle Holocene *A. cervicornis* are limited due to flooding of reef outcrops during Holocene sea-level rise. While 400–500 yr gaps in Holocene *A. cervicornis* growth have been observed locally (Shinn et al., 2003), it has been suggested that the recent large-scale decline of *A. cervicornis* may be without precedent (e.g., Aronson and Precht, 2001). Discerning patterns of *A. cervicornis* resilience or decline during the Holocene should prove valuable in determining the susceptibility of this species to a variety of natural and anthropogenic stresses.

This paper presents a closely dated, outcrop-based, multiproxy paleoenvironmental study of early to middle Holocene aragonitic *A. cervicornis* reefs to better understand conditions favorable for sustained growth of this species. Geochemical and sedimentological data indicate that early to middle Holocene *A. cervicornis* thrived despite changes in temperature, salinity, storm activity, and base level. Our data imply that this species may be more resilient to environmental variability than previously thought, and support the proposal that the recent decline of this key reef-builder is due to unprecedented ecological pressures related to anthropogenic activity.

GEOLOGIC SETTING

The Enriquillo Valley, southwestern Dominican Republic, contains outcrops of geochemically pristine, subaerial Holocene coral reefs (Mann

et al., 1984). Rising postglacial seas flooded the valley, forming a marine embayment with extensive fringing reefs as early as 9.38 ka. Normal marine conditions were terminated by ca. 5 ka, likely due to climate and tectonic activity (Mann et al., 1984; Taylor et al., 1985). Lago Enriquillo, a remnant of the paleoembayment, currently is at ~42 mbsl. Fossil reef outcrops containing at least 28 coral species (Stemann and Johnson, 1992) are exposed in gullies along the lake margin. In arroyo Las Clavellinas (18°30.077'N, 71°32.800'W), above the north-central Lago Enriquillo coast, *A. cervicornis* is the dominant coral within the upper (paleoshoreward) reaches of the fossil reef. The best-exposed *A. cervicornis* bed at Las Clavellinas is ~11 m in height, and multiple exposures allow a three-dimensional sampling of reef material (Fig. 1).

METHODS

Acropora cervicornis specimens were sampled in outcrop for geochemical analyses at 10 and 2 cm intervals (Fig. 1), and 48 bulk coral/sediment samples were collected for taphonomic analysis by excavating 20 × 10 cm sections of outcrop at three Las Clavellinas locations. Three taphonomic sample locations were chosen to represent the oldest, deepest-water deposits, contemporaneous shallow-water deposits up paleoslope, and the youngest coral growth at Las Clavellinas. Elevations for all samples are reported relative to a year 2000 benchmark (Greer and Swart, 2006). Taphonomic values were assigned in the field based on a grade scale of 1 (pristine) to 5 (poor preservation; adapted from Greenstein and Moffat, 1996) that factored corallite and fine-scale skeletal preservation, porosity, angularity of broken edges or skeletal protrusions, and friability.

X-ray diffraction was used to determine carbonate mineralogy of corals. Only 100% aragonite samples were used for radiocarbon or geochemical analyses. High-resolution samples for stable isotope determination were generated from coral slices using computer-controlled micromilling devices at either 1000 μm or 250 μm intervals along axial or corresponding lateral corallites. Low-resolution samples were collected by milling 2500 μm transects parallel to the axial corallite or by homogenizing ~0.5-cm-diameter sections of individual corals proximal to the axial corallite. Samples were analyzed using a Kiel-III carbonate preparation device directly coupled to a Thermo-Finnigan MAT 252 in the University of Saskatchewan Isotope Laboratory.



Figure 1. The Las Clavellinas *Acropora cervicornis* facies. **A:** Sampling the near-continuous 2000 yr section at 10 cm intervals. Ages given are estimated. **B:** Close-up of *A. cervicornis* specimens (note rock hammer for scale). The apparent angular discordance in bedding mid-outcrop is not depositional but rather a function of erosion and camera angle.

Fifty-eight *A. cervicornis* samples were radiocarbon dated, with 47 from 10 cm intervals at the basal Las Clavellinas section (Figs. 1 and 2), seven additional samples from Las Clavellinas, and three from two adjacent Enriquillo sites (18°32.020'N, 71°37.202'W; 18°32.576'N, 71°47.968'W). Calibrated ages were derived using CALIB v5.0.2.html and the ratified Marine 04 calibration data set. We estimated the reservoir age to be similar to published results for the Dominican Republic and used a ΔR of ± 50 yr. Forty-two samples from the basal Las Clavellinas section were analyzed for Sr/Ca ratios at Lamont Doherty Earth Observatory using ICP-OES (Fig. 2). Raw Sr and Ca concentration data were drift corrected, and the relative standard error for replicates was less than $\pm 1\%$.

RESULTS

Radiocarbon dates from the thickest Las Clavellinas section show 9.2 m of continuous *A. cervicornis* accumulation between 9.38 ka and 7.32 ka (Fig. 2), with the largest potential gap at ca. 8 ka and a few mixing events, the most prominent centered at ca. 8.6 ka. Additional dates from Las Clavellinas show *A. cervicornis* growth to 5.85 ka with no coral species replacement. Dates from adjacent sites indicate *A. cervicornis* growth at 5.70 ka and 5.38 ka.

Corals at the base of two Las Clavellinas sections on either side of the arroyo (9.38 and 9.36 ka) lie 6 m apart vertically and ~ 20 m horizontally. Since there is no evidence of deformation at Las Clavellinas, it appears that *A. cervicornis* colonized a steep slope. Taphonomic grades were assigned to 2778 individual *A. cervicornis* coral samples collected at Las Clavellinas to assess physical conditions and degree of in situ preservation with relative paleodepth and time. Samples from the basal Las Clavellinas section have a mean taphonomic value of 3.4 ($\sigma = 0.90$). The lower

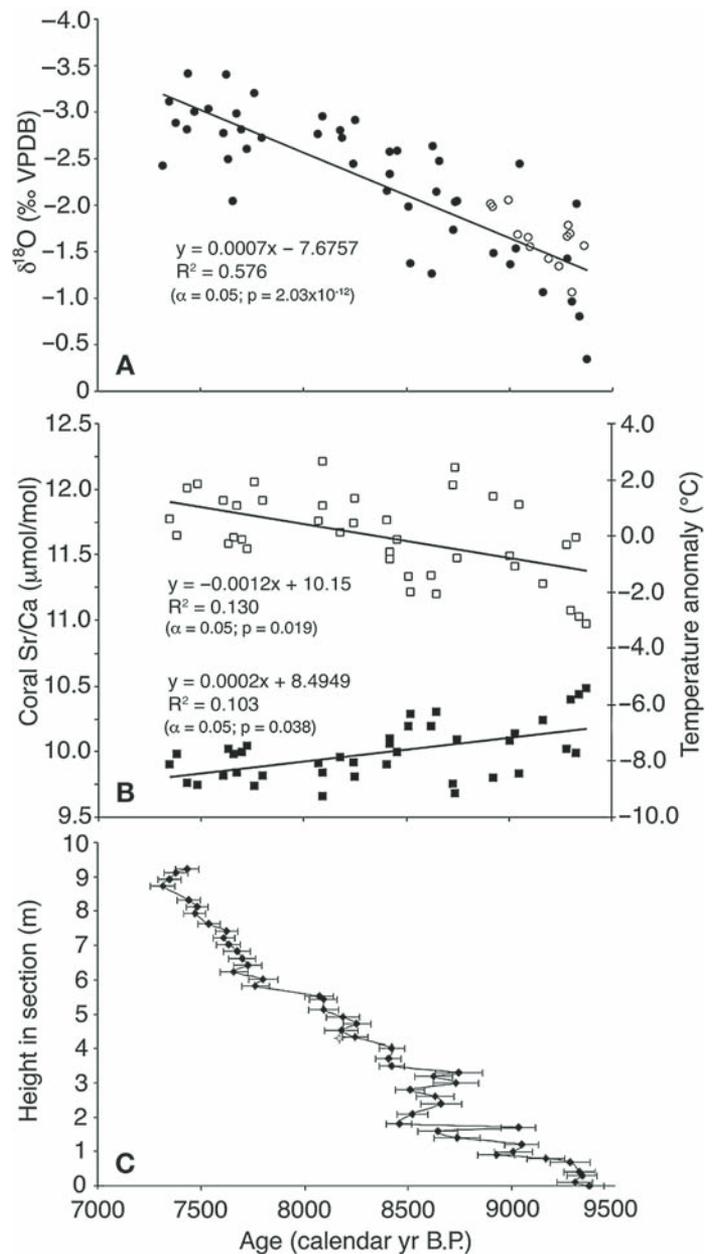


Figure 2. Geochemical data from Las Clavellinas *Acropora cervicornis* samples. **A:** $\delta^{18}\text{O}$ values from bulk (closed circles) and mean high-resolution (open circles) data from individual corals. Linear regression shows a significant trend ($p < 0.001$). **B:** Sr/Ca ratios (closed squares) and temperatures (open squares) calculated using the Reynaud et al. (2007) Sr/Ca-SST calibration for *Acropora* spp. **C:** Calibrated radiocarbon ages plotted with 1σ error bars.

100 cm of a shallower contemporaneous section yield a mean taphonomic value of 2.9 ($\sigma = 0.93$), and the upper 100 cm are characterized by higher and more consistent taphonomic values (3.8 mean, $\sigma = 0.66$). The youngest corals sampled at the top of the Las Clavellinas section have a mean value of 3.6 ($\sigma = 0.66$) (GSA Data Repository¹).

$\delta^{18}\text{O}_{(\text{CaCO}_3)}$ data (Fig. 2) represent 319 Las Clavellinas measurements collected at various resolutions. High-resolution $\delta^{18}\text{O}_{(\text{CaCO}_3)}$ data from indi-

¹GSA Data Repository item 2009067, age, taphonomy, and additional isotope data, is available online at www.geosociety.org/pubs/ft2009.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

vidual corals were averaged to show a 2000 yr trend in mean $\delta^{18}\text{O}$ values, which decrease by up to 3‰ from 9.38 ka to 7.32 ka. Additional $\delta^{18}\text{O}_{(\text{CaCO}_3)}$ data ($n = 242$) from two younger Las Clavellinas corals show $\delta^{18}\text{O}$ values of -2.6‰ (5.85 ka) and -2.9‰ (5.70 ka). Mean Sr/Ca decreases in value over the same time span from ~10.50 to ~9.75 $\mu\text{mol/mol}$ (Fig. 2).

DISCUSSION

Radiocarbon data show near-continuous accumulation of *A. cervicornis* for ~2000 yr with continued *A. cervicornis* growth to at least 5.70 ka and possibly 5.38 ka. Geochemical data suggest the species dominated areas of the Enriquillo reef despite environmental changes through the Holocene Thermal Maximum (HTM; Sandweiss et al., 1996) and the hypothesized migration of the Intertropical Convergence Zone (ITCZ; Haug et al., 2001). A perceived break in the Enriquillo record at 7.32 ka is due to sampling constraints, and only one potential gap in coral accumulation (ca. 8 ka) may exist in the ~2000 yr section. From 9.38 to 5.61 ka, there is no evidence for wholesale species turnover events such as those documented by Aronson et al. (2002) and seen on reefs today. While distribution of *A. cervicornis* can be dynamic in time and space, Enriquillo *A. cervicornis* was seemingly able to persist without the marked ecological shifts seen in modern times (Davis, 1982), although it is possible that ecological shifts occurred but were too short-lived to be recorded. Environmental conditions likely experienced by Las Clavellinas corals are discussed below.

Temperature and Precipitation

Increasing summer insolation led to early Holocene Northern Hemisphere warming (Berger, 1978), with temperatures peaking at the HTM (ca. 6 ka) in the tropics (e.g., Hodell et al., 1991; Haug et al., 2001). It is generally agreed that tropical HTM temperatures were within 1–2 °C of present values (Sandweiss et al., 1996; Farmer et al., 2005). Therefore, Enriquillo *A. cervicornis* flourished in temperatures close to, if not exceeding, those of present day. However, the large and variable decrease in *A. cervicornis* $\delta^{18}\text{O}$ values from 9.38 to 7.32 ka is not likely a result of temperature change alone. Contribution of ice volume to seawater $\delta^{18}\text{O}_{(\text{H}_2\text{O})}$ was small by the early Holocene (Guilderson et al., 2001). If the decrease in Las Clavellinas $\delta^{18}\text{O}_{(\text{CaCO}_3)}$ is solely ascribed to temperature, the 3‰ shift in values between 9.38 and 7.32 ka would reflect a sea-surface temperature (SST) change of ~8 °C, as estimated using a culture-based $\delta^{18}\text{O}$ -SST calibration (0.34‰ per °C) for *Acropora* spp. from Reynaud et al. (2007). Estimates using less conservative paleotemperature equations for *Acropora* spp. (Guilderson et al., 1994) yield even less realistic temperature ranges. A Sr/Ca-SST-derived calibration for *Acropora* spp. used to cross-check $\delta^{18}\text{O}$ -inferred paleothermometry (Reynaud et al., 2007) implies a more realistic ~2–3 °C (Sr/Ca-based) temperature increase from 9.38 to 7.32 ka (Fig. 2). While still large in magnitude relative to ~4.5 °C western Atlantic temperature increases since the Last Glacial Maximum (Guilderson et al., 1994, 2001), the Sr/Ca-inferred SST range may be reasonable. Therefore Sr/Ca data support that temperature is not the sole driver of $\delta^{18}\text{O}_{(\text{CaCO}_3)}$ variability in these corals.

$\delta^{18}\text{O}_{(\text{CaCO}_3)}$ values of corals can be controlled by precipitation/evaporation patterns as well as temperature (e.g., Swart and Coleman, 1980). A potential cause of decreasing $\delta^{18}\text{O}_{(\text{H}_2\text{O})}$ in the early to middle Holocene may be a northward displacement of the ITCZ during insolation-related Northern Hemisphere warming (Haug et al., 2001). A more northern summer extent of the ITCZ might have trapped isotopically light precipitation in the Atlantic Basin via reduced vapor transport to the Pacific (Stott et al., 2004). A more northern ITCZ may also have resulted in increased summer precipitation in the mountainous Enriquillo Valley region, decreasing $\delta^{18}\text{O}_{(\text{H}_2\text{O})}$ of the embayment via orographic effects.

The wide range in $\delta^{18}\text{O}_{(\text{CaCO}_3)}$ values in Enriquillo corals could imply a highly variable precipitation regime and the inconsistent influx of freshwater associated with storm-related changes in the hydrology

of the Holocene embayment (Greer and Swart, 2006), as well as annual changes in ITCZ extent. Variations in $\delta^{18}\text{O}_{(\text{CaCO}_3)}$ values of up to 1.5‰ are not uncommon within single Las Clavellinas coral specimens sampled at high resolution. Therefore, $\delta^{18}\text{O}$ values from these early to middle Holocene corals do not reflect temperature but rather a transition from cool/dry to warm/wet conditions. $\delta^{18}\text{O}_{(\text{CaCO}_3)}$ values from HTM corals (5.70 and 5.85 ka) indicate a stabilization of temperature and/or precipitation consistent with peak temperatures and maximum ITCZ extent before cooling and southward migration of the ITCZ. Stable isotope records from nearby Lake Miragoane, Haiti, corroborate this transition (Hodell et al., 1991), and geochemical data from massive Enriquillo corals (Greer and Swart, 2006) and microfossils (Medley et al., 2007) support the interpretation that the paleoembayment was subject to variable Holocene salinity as well as temperature changes.

Relative Sea Level, Storms, and Wave Energy

Mixing events and abundant physical and theoretical evidence suggest Enriquillo reefs were subjected to periodic tropical storms and hurricanes (Guerard et al., 2004) while flourishing in rapidly rising early Holocene seas. Taphonomic analyses reveal contemporaneous growth within a 6 m depth range. Data from deeper-water, older reef sections (ca. 9.4 ka) could imply a relatively protected paleoenvironment (lower taphonomic mean, higher variance) below the fair-weather wave base. The youngest section (ca. 5.9 ka) is dominated by slightly higher taphonomic values and lower mean standard deviation, which may indicate that the corals had reached the fair-weather wave base in a time of rapidly diminishing accommodation space and slowing sea-level rise.

Proposed Causes of Recent Collapse

Our data show that Holocene *A. cervicornis* was capable of thriving for thousands of years under highly variable temperature and salinity conditions. When proposed factors for the present-day decline are considered, our data support, via a process of elimination, white-band disease, a bacterial infection specific to acroporids (Antonius, 1981), and/or multiple anthropogenic stressors *not* related to temperature, salinity, storms, or sea-level rise as cause(s) for *A. cervicornis* collapse (Harvell et al., 1999; Aronson and Precht, 2001; Jackson, 2001; Hughes et al., 2003; Pandolfi et al., 2005). At this time, these remaining factors cannot be assessed from fossil coral material.

While our study cannot identify a single cause for current *A. cervicornis* mortality, these data may be helpful in ruling out most natural (nonanthropogenic) forces as primary drivers for *A. cervicornis* collapse. This supports the contention that stressors not present earlier in the Holocene, such as eutrophication, ocean acidification, and fishing pressures, may now be forcing *A. cervicornis* to threshold conditions unfavorable for sustained growth (Jackson, 2001; Hughes et al., 2003; Pandolfi et al., 2005; Hoegh-Guldberg et al., 2007). This study implies that the present warm climate is not a primary driver for *A. cervicornis* collapse, but we cannot rule out the possibility that the current *rate* of warming may be different from that of the middle Holocene or that future warming beyond middle Holocene temperatures might prove devastating to a species already impacted by additional stressors.

CONCLUSIONS/IMPLICATIONS

Data presented here, at high spatial and temporal resolution, document virtually continuous *A. cervicornis* growth for at least ~2000 yr in the early to middle Holocene and support interpretations of anomalous recent decline (Hubbard et al., 1994; Greenstein et al., 1998; Aronson et al., 2002). Geochemical, age, and taphonomic data from Holocene *A. cervicornis* reveal a resilient coral species at variable depth regimes thriving in a time of rapid sea-level rise, SSTs likely similar to present, changes in precipitation associated with ITCZ migration, and a transition from cooler/drier to warmer/wetter central Caribbean climate. Any

potential breaks in deposition were not accompanied by the ecological shifts in coral species dominance seen in the modern and late Holocene fossil record (Aronson et al., 2002). Our data suggest that variations in temperature, precipitation/salinity, storms, and base level did not result in *A. cervicornis* collapse in the past and that drivers for the current decline must be outside those environmental and climatic factors that were operative in the early to middle Holocene. This suggests that anthropogenic factors and increased incidence of disease (unrelated to warming) may be responsible for the current decline. This study amplifies concerns that a once-hardy keystone coral species may be at the brink of extinction today. Furthermore, it reinforces the need to invest in a multipronged approach to coral reef protection from local anthropogenic stressors (Pandolfi et al., 2005), and supports continued efforts to understand the potential impacts of anthropogenic activity on the virulence of white-band disease.

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