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PROCEEDINGS OF THE TWENTY-FIFTH ANNUAL KECK RESEARCH SYMPOSIUM IN GEOLOGY

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Keck Geology Consortium: Projects 2011-2012
Short Contributions— Virgin Islands Project

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DEPTH-RELATED CARBONATE CYCLING IN A MODERN REEF: ST. JOHN, U.S. VIRGIN ISLANDS

DENNIS K. HUBBARD, Oberlin College
KARLA PARSONS-HUBBARD, Oberlin College

INTRODUCTION

The literature is replete with discussions of coral-reef decline in response to human exploitation, overfishing, nutrient loading and, most recently, climate change (Hoegh-Guldberg et al., 2007; Hughes, 1994; Pandolfi et al., 2011; Pandolfi et al., 2005). Over the past decade, discussions have increasingly considered whether the constructive processes that have built Holocene reefs might be supplanted by bioerosion, the aggregate destruction of reef surface by grazing and burrowing organisms. Recent investigations suggest that this may already be occurring and that Caribbean reefs are becoming flatter and less spatially complex in response to accelerating destructive processes (Alvarez-Filip et al., 2009). This will have significant consequences for both the organisms that inhabit the reef and humans living near them.

Each successive report of the Intergovernmental Panel on Climate Change (IPCC) reflects greater certainty regarding anthropogenic influence and paints a grimmer picture of the future than its predecessor. The highest point in the Marshall Islands is only 3.3 m above sea level and eighty percent of the land in the Maldives is even lower (Al_Jazeera, 2010) - while reefs are building at rates that are perilously close to recent estimates of sea-level rise (Church and White, 2011).

It has been widely assumed that, because carbonate production by corals is strongly depth-dependent, reef accretion will follow a similar pattern. However, a recent summary of Holocene reef-building in the Caribbean concluded that this is not the case - reefs have built at an average rate of ~3.5 mm/yr over the past 10,000 years, but those close to sea level have built no faster than their counterparts in 20-30m of water (Hubbard, 2009). One explanation for this counterintuitive finding is that higher carbonate production by shallow-water corals is offset by higher bioerosion, which would be driven by many of the same depth-dependent factors. Also, the detrital by-products of biologically driven degradation will move downslope, adding to the volume of deeper reefs as sediment is bound up by encrusters and submarine cement.

All of these issues require a better quantitative understanding of the balance between construction and destruction on modern reefs and how that might be changing. While our understanding of the factors involved is reasonably complete, quantitative summaries have been sparse (Hubbard et al., 1990; Scoffin et al., 1980; Stearn et al., 1977). We have reliable rates for coral growth based on both direct measurements and the examination of annual bands that are akin to tree rings but are revealed only in X-rays of coral slabs. Similarly, we can calculate the accretion rates of Holocene reefs using radiometric dating of samples recovered from cores. However, reliable rates of bioerosion and encrustation are more illusive. Samples from the reef provide important information on the volumes of material removed by different organisms. However, we do not know when erosion began and, therefore, cannot compute an actual rate. Attempts to solve this problem have involved artificial limestone substrates deployed for known times. It remains unclear, however, whether a block of carbonate attached to the reef surface or placed on an experimental rack nearby will respond in the same way as a recently exposed, natural reef surface.

The primary goal of the St. John Keck Project was to examine all of these factors along a known depth gradient. What is unique is that we could use detailed monitoring data by the National Park Service to constrain the time of death for individual coral samples. As a result, researchers were able to attach a reliable rate to the patterns they observed. As a result, their efforts provide a reliable assessment of carbonate

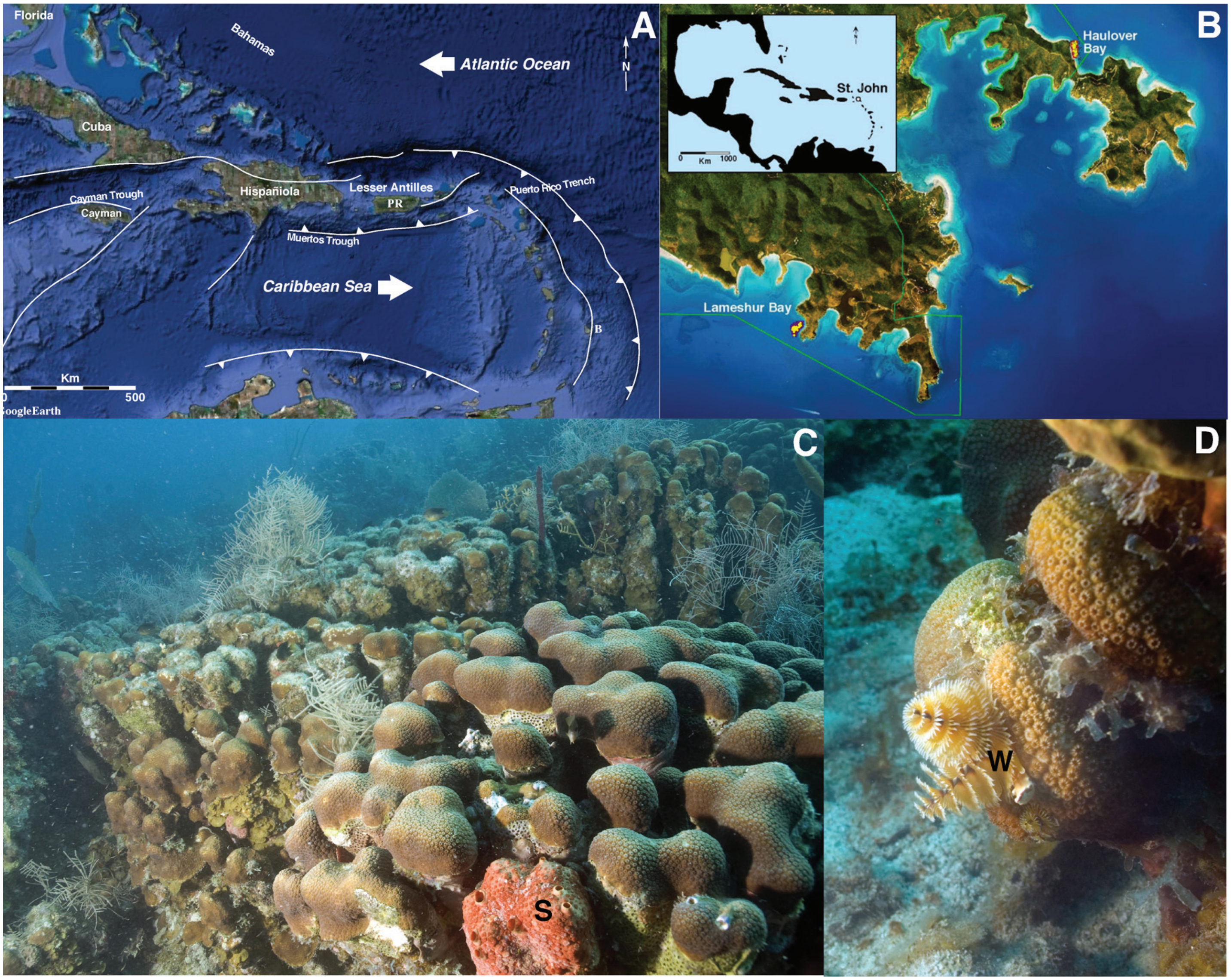

Figure 1. A) GoogleEarth image showing the large-scale bathymetry of the eastern Caribbean. Major faults show the complex tectonic regime of the region. The location of St. John is shown (STJ). B) GoogleEarth image of eastern St. John showing the locations of Haulover and Lameshur Bays on the north and south coasts of St. John, respectively. Sample sites in Haulover Bay and along Tektite reef in southeastern Lameshur Bay are show by the shaded yellow. C) Underwater photograph of Tektite reef at a depth of ca. 15m. The knobby corals in the foreground are Montastraea annularis. Many colonies in the background (duller brown to white) are dead. Note the common cryptic depressions separating each coral knob. The red substrate in the foreground is a sponge (s) that is boring into the coral interior. D) Close-up underwater photograph of Montastraea cavernosa colonies and boring worms (w).

cycling without using artificial substrates or manipulative experiments to characterize changes in the reef.

STUDY AREA

The Virgin Islands sit along the northern boundary between the Caribbean Plate and the North Atlantic Plate (Fig. 1a). St. John, the smallest of the three main U.S. Virgin Islands, is dominated by Cretaceous volcanic rocks. Active tectonism has resulted in generally steep slopes on land and along the adjacent insular shelf. The result is smaller fringing reefs closer to shore where adverse impacts related to human habitation are maximized. While half of the land on St. John sits within Virgin Islands National Park, runoff from roads and other park-related infrastructure still negatively affect the reefs within its jurisdiction. Fishing is officially prohibited within the

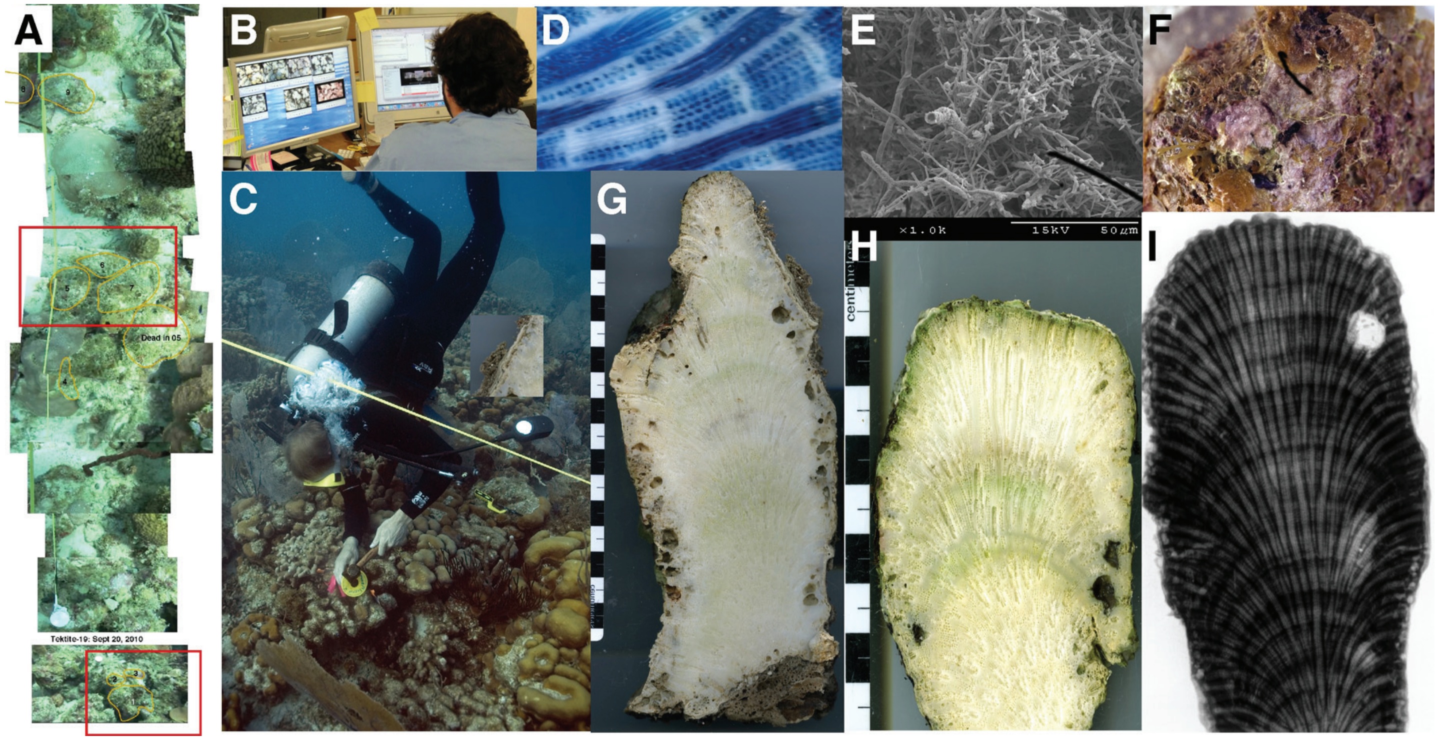

Figure 2. A) Mosaic of Transect T-19 from Lameshur Bay. Individual frames were captured from monitoring video. Each coral was examined in each video to determine the last time it was seen alive. B) Successive videos (left screen) were used to identify the time-of-death for corals along each transect. C) Diver collecting predetermined coral samples from the reef. D) Close-up of a coral chip impregnated with blue epoxy (top is to the right). The thicker white bands (left to right) are the walls of the calyx in which coral polyps lived. The perpendicular tabulae divide the calyx into smaller chambers that provide structural strength for the overall colony. The smaller meshwork reflects coral septa, vertical ridges that likewise provide structural integrity. The chip is ca 5 cm from left to right. E) SEM photograph along one of the calical walls shown in (D). Each tube is a cast of the tunnels made by micro-borers (the smaller ones are probably fungi; larger tubes are probably from algae or cyanobacteria). The chip in (D) was dissolved in acid and what is seen in this photo is the resin cast that remains. Contributions by Neal and Rogers (this volume) provide information on community structure and substrate removal by these and other micro-bioeroders. F) Close-up photograph of macroalgae (brown, probably Turbinaria) and crustose coralline algae (pink) along the edge of a dead coral sample. Multiple photos were taken of each sample within 24 hours to record original color as well as soft organisms that would eventually be lost during drying and sample processing. McElroy (this volume) quantified the patterns and rates of carbonate production by calcareous epibionts that developed after each coral died. G) Coral slab showing macro-bioeroder galleries (mostly along the sides) of a colony of Montastraea annularis. Whitcher (this volume) quantified the contribution of each bioeroder group along the tops and sides of typical colonies. Note also the green bands related to algae incorporated in the coral skeleton, probably while the colony was alive. H) Slab of a coral sample showing well-developed algal bands (probably Ostreobium spp.) that may be associated with past episodes of coral bleaching (see Clarke, this volume). I) X-radiograph of a coral sample. The dark, radiating lines are the calical walls shown in (D). The lighter and darker areas reflect density patterns within the coral. Each dark band reflects denser skeleton laid down in late summer/fall when warmer water accelerated skeletogenesis. Benson (this volume) used growth rates determined from coral X-rays and quantitative data on coral cover collected from each video-survey to compute the changing carbonate production along each transect. His data on substrate type (live coral; dead coral, limestone pavement, sand) will eventually be used to convert the data from all the Keck-STJ projects into a detailed carbonate budget for the reefs of eastern St. John.

park, but numbers of grazing fish that normally keep algae in check are still depressed. In addition, increasing water temperature associated with global climate change has triggered increased disease and "coral bleaching". In the latter phenomenon, corals expel photosynthetic symbionts that normally reside within their tissues. The pigments carried by these zooxanthellae give corals their bright colors and, without them, the coral tissue is clear and gives a view of the white skeleton beneath – hence the term "bleaching". As coral abundance has declined, so has the amount of carbonate they normally create. As a result, the balance between calcium-carbonate production by corals (Fig. 1c) and post-mortem bioerosion by fish, sponges and worms (Fig. 1c, d) has gradually shifted in favor of the latter.

Since 2003, the National Park Service (NPS) has been monitoring reef change along 30 permanently marked transects in Haulover and Lameshur Bays on eastern St. John (Fig. 1b). Changing coral cover has ben quantified using video surveys that are repeated at each site. In the summer of 2011, 73 dead coral samples were collected along 11 of these transects to examine carbonate cycling along a depth gradient between 5 and 20 meters (Table 1). The NPS videos were used to generate a mosaic for each transect (Fig. 2 a,b). The time of death for each sample was determined using the successive video surveys. A particularly severe bleaching and disease outbreak in the summer of 2005 caused a massive coral die-off that was documented in the bi-monthly monitoring surveys. Most of our samples died in this event and the initiation of post-mortem alteration is, therefore well constrained, allowing the first quantitative assessment of bioerosion in samples that remained in place after a natural event and responded solely to the natural conditions that followed.

Sampling - Using the maps created from the NPS videos, divers chose samples that could be removed without otherwise disturbing the surrounding substrate. This was particularly important as these transects would continue to be used in the long-term

			Coral Cover (%)		
Bay	**Transect**	**Depth (m)**	**Jan-03**	**Jan-10**	**Samples**
Haulover	H-08	4.9	25.2	9.0	6
	H-14	6.1	32.1	24.1	8
	H-15	7.6	35.2	14.1	7
			Sept-05	**Nov-09**	
Lameshur	T-15	7.6	32.9	5.2	15
	T-16	10.1	14.8	3.5	4
	T-17	11.6	12.8	3.7	5
	T-12	12.2	44.8	20.2	5
	T-06	14.0	31.4	22.5	4
	T-07	15.5	21.1	14.8	5
	T-19	18.3	23.4	12.5	7
	T-20	19.2	12.4	12.5	7

Table 1. Summary data for eleven transects along which coral samples were collected for this study.

monitoring program. Each sample was tagged and its character was documented in still photographs and underwater video. Samples were carefully collected with a hammer and chisel (Fig. 2c). At the surface, each sample was photographed to document the benthic cover while colors and non-calcareous epibionts were still fresh (Fig. 2f). In the lab, samples were slabbed and scanned at high resolution for permanent documentation (Fig. 2g, h).

STUDENT PROJECTS

Carbonate Production by Corals – One project (Benson) used successive videos for each transect (Fig. 2 a,b) to track changes in live-coral cover over the monitoring period. Slabs from two corals along each transect were X-rayed to reveal the annual banding pattern (Fig. 2i). The freeware program NIH ImageJ was used to determine the average linear-extension rate for each coral. The weight and volume of two chips cut from the same corals were used to determine their bulk density, and this was used to compute the annual carbonate production by corals along each transect. This project also provided a quantitative measure of changes (mostly increases) in the surface area over which carbonate loss and gain reported by other investigators was distributed. These data will eventually be combined into an overall carbonate budget that quantifies changes in carbonate production and destruction on St. John reefs since 2005.

Encrustation – Another project (McElroy) quantified the types and extent of encrusting bionts on the same dead coral samples (Fig. 3f). Multiple estimates of cover by the major biont groups (encrusting coralline algae, sponges, algal turf, macroalgae and foraminifera) were made along the tops and sides of each coral plus a transitional area separating the two. In addition, the thickness of any calcareous crusts was measured for each sample to compute the amount of carbonate that was added after the death of each coral, mostly by corallines and foraminifera.

Macroboring – Cross-sectional slabs from 33 samples were examined at low magnification to identify the relative importance of macro-borers. Each slab (Fig. 2g) was examined closely at low magnificantion under a dissecting microscope, and individual bioeroder galleries were delineated on the high-resolution scan of the slab. Each cavity was attributed to one of the major bioeroder groups (sponges, molluscs, worms) and the total volume of material removed by each group was quantified using NIH ImageJ. Based on the known times of death, this project (Whitcher) quantified the rates of bioerosion for the last 5 years. This represents the first detailed measurement of biological substrate destruction using natural substrates that have not been manipulated as part of the experimental set-up.

Microboring - Subsamples were taken from the coral surface of selected slabs. Tissue was removed, the chips were dried and the samples were impregnated with a colored epoxy resin at high pressure. Samples were etched in weak (5-10%) HCL to decalcify the coral within the resin block. When viewed under SEM, the resin stands out as a cast to clearly show the geometry of the infaunal borings of algae, cyanobacteria and fungi (Fig. 2e). One study (Rogers) characterized the structure of the infaunal community across the depth range of the study. Another (Neal) quantified the rates of substrate destruction by water depth.

Biological and Geochemical Proxies for Coral Bleaching – As described above, recent increases in water temperature have resulted in severe coral bleaching. Recent studies suggest that, when this happens, more light is transmitted to the interior of the coral colony and light-sensitive bacteria like *Ostreobium* spp. can proliferate. When this happens, a distinct green band is left behind that is clearly visible when the coral is slabbed (Fig. 2h). These mimic the density bands revealed in X-rays (Fig. 2i) but are not necessarily coincident with them. Because coral skeleton will be in equilibrium with the fluid in which it is precipitated, the presence of different photosynthesizing species may change the immediate water chemistry and leave distinct isotopic signatures behind that can be used to identify past thermal stress events. Clarke examined this phenomenon by collecting closely spaced skeletal samples with a micromill and subjecting them to analyses of oxygen (a temperature/salinity proxy) and carbon isotopes (a proxy for carbon source) across visible green algal bands like those seen in Figure 2h.

LARGER PROJECT GOALS AND ACCOMPLISHMENTS

Individually, each project has provided valuable information about the production, destruction and cycling of calcium carbonate in two modern reefs over a time period in which community structure has changed dramatically. Because the samples from which our measurements were taken have not been experimentally manipulated, the data outlined in the following Short Contributions provide one of the best estimates of reef- and organism-scale processes to date. This information can be compared to core data from the Holocene and can also be used to assess the validity of assumptions that have been made about the applicability of artificial experiments to what is actually occurring within the reef. Geochemical studies have examined small-scale isotopic changes within the context of a well-documented record of changing reef-community structure over time – in particular, the timing of thermal stress responses on a coral-by-coral basis.

In addition to providing valuable information on a host of individual reef processes, these studies will allow us to create a detailed carbonate budget for these two reefs using data collected within a common framework of space (depth) and time (each monitoring survey). Collectively, data from the corals collected on St. John are already showing that our picture of how and where important processes are occurring is oversimplified. Most monitoring studies quantify changes in plan view, as might be done using a quadrat (a 1-m^2 frame laid on top of the reef surface) or a transect stretched between permanent survey points. Over the past three decades, it has become increasingly apparent that reef structure is not two-dimensional and that such methods yield inaccurate results. Both the production and destruction of carbonate also occur on "meso-scales" (i.e., down in the cracks between coral heads) and "micro-scales" (within complex coral calices) that have been recognized but largely ignored. When we fail to recognize the importance of bioerosion along these irregularities, substrate removal is disproportionately underestimated. The careful characterization of changes in the relative importance of areas where carbonate is created and removed can be combined with other Keck-STJ studies of substrate alteration and the geometry of the surfaces along which it occurs to construct a much better model of carbonate cycling in reefs. These models and the possible geochemical proxies for past stress events can be applied to increase our understanding of past reefs as well as the possible future of those structures in the immediate future.

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