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A HYPOTHESIS FOR BIOGENIC CAVE FORMATION: A STUDY CONDUCTED IN THE BAHAMAS

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ABSTRACT

The currently accepted hypothesis for the development of caves in carbonate islands and coastal areas suggests that mixing of $CaCO_3$ supersaturated seawater with $CaCO_3$ saturated groundwater creates undersaturated mixed water that is thought to be responsible for large-scale carbonate dissolution. This hypothesis does not address the dissolution potential of rainwater descending through the vadose zone, or the groundwater. It is known that soon after rainwater has moved through the soil and makes contact with the underlying limestone it becomes buffered by dissolution of $CaCO_3$. We hypothesize that the dissolution capacity of the vadose water is primarily controlled by the assimilation of CO_2 produced by heterotrophic bacteria living in the pores of the host rock.

Rainwater that was collected before it made contact with the ground on San Salvador Island, Bahamas contained 10^3 bacterial cells per milliliter. In contrast, water collected from dripstones in caves contained $>10^4$ to 10^5 colony-forming-units (cfu). Wall-rocks collected from dry caves on the island, contained $>10^6$ cfu, and the dominant heterotrophic bacteria are in Order Actinomycetales, which are known to produce CO_2 and NH_3 as end-products of their metabolism. The presence of these microbial populations, comprising at least 16 different species, provides a significant potential for the production of CO_2 and other microbially generated acids. Surface and 2.5-cm-deep wall-rock samples sealed in sterile vials for 14 days yielded a CO_2 content that ranged from 770 to 410 ppm above the current atmospheric concentration (~380 ppm).

Our observations suggest that bacteria are maintaining and driving the CO_2-related dissolution in the vadose and phreatic zones. It is also likely that secondary porosity and permeability may be enhanced even during periods when the rock is not saturated with water.

Limestone in the phreatic zone, especially where they are exposed to the mobile mixing-zone water, experience the greatest removal of solutes and the greatest concentrations of bacteria. As a result, it is reasonable to suppose that void enlargement reaches the highest rates in association with those environments. Hence, caves develop and enlarge to their greatest extent at or near sea level, which is consistent with the flank margin hypothesis. This can also explain why caves that experienced only relatively short episodes of phreatic conditions can be so large.

INTRODUCTION

In the 1980s, research in the Bahamas revealed that there are many large caves with morphologies that indicate phreatic dissolution that occur in rocks that are only ~330,000 to 120,000 years old. In addition, those rocks have been subjected to phreatic conditions only during one or more of the short (~10,000 years) glacio-eustatic sea-level highstands that occurred in the Mid-Late Pleistocene (Mylroie and Carew, 1988a). Thus, some of these caves must have formed in no more than 10,000 to 12,000 years, and none represent more than 45,000 years of dissolution in the phreatic zone. In an attempt to explain how such large caves could have formed during such short intervals of time, the flank margin hypothesis was proposed by Mylroie and Carew (1990).

The generally accepted view of limestone dissolution is that it is due to the infiltration of low-pH meteoric water and groundwater that results from incorporated atmospheric CO_2 as well as CO_2 from the near-surface (e.g. soil) environment; and it is these initial CO_2 concentrations that dictate the amount of limestone dissolution (White, 1988). It has been assumed that once meteoric water charged with atmospheric and soil CO_2 enters the vadose zone, continuing input of meteoric water keeps this water undersaturated with respect to $CaCO_3$, and thereby maintains its dissolution potential.

It has been noted (Mylroie and Carew, 1990; White, 1988) that there is a large volume of literature linking the formation of caves and the water table. It has also been suggested that the mixing of different water masses that are saturated, or even supersaturated, with respect to $CaCO_3$, can produce undersaturated mixed water capable of significant dissolution of limestone (Plummer, 1975; Mylroie and Carew, 1990; White, 1988; Back et al., 1986; Sanford and Konikow, 1989). It has been further noted (Mylroie and Carew, 1990; White, 1988; Back et al., 1986; Sanford and Konikow, 1989; Stoessell et al., 1989) that dissolution often is most extensive where mixtures of freshwater and seawater are discharging into the sea. However, studies of the hydrogeochemistry of Bermuda (Plummer et al., 1976) demonstrated that calcite saturation in the mixing zone is controlled by CO_2 degassing, and not by the mixing of freshwater with seawater. The source of the CO_2 necessary for driving the dissolution process has not been idenfied.

The flank margin hypothesis of cave formation (Mylroie and Carew, 1990) proposes that the mixing of different water masses saturated with respect to $CaCO_3$ under different conditions is responsible for the rapid cave development seen on these islands. In particular, maximum dissolution is proposed to occur at the discharging margin of the freshwater lens due to the close juxtaposition of the top of the groundwater lens (where vadose water mixes with the fresh to brackish groundwater lens), and at the base of the lens (where fresh to brackish groundwater mixes with underlying seawater).

Currently, the flank margin hypothesis is the only accepted explanation for the development of such caves, and the model has been extended to carbonate islands throughout the world (Frank et al., 1998 ;Mylroie and Carew, 1995; Mylroie et al., 1995; Mylroie et al., 2001). However, we argue that this hypothesis does not address fully the actual dissolution potential of rainwater as it migrates downward through the vadose zone and merges with the groundwater. In addition, it does not correctly identify the actual cause of mixing zone corrosion. We postulate that the dissolutional capacity of the vadose water is enhanced or maintained as the descending meteoric water accumulates microbially-generated CO_2 that is produced by heterotrophic bacteria residing in the pores of the host rock. That is, from the time

rainwater enters the rock to the time it merges with the groundwater at the water table, bacteria living in rock pores (Schwabe et al., 1996) recharge the descending water with CO_2. In addition, bacteria in the fresh, mixed, and marine groundwater also contribute CO_2 and produce other organically generated acids that contribute to the dissolution of carbonate rocks (Schwabe, 1999; Schwabe, 2002). In particular, accumulations of particulate organic carbon (POC), particulate organic matter (POM), dissolved organic carbon (DOC), and bacterial cells at the major density interface at the upper mixing zone boundary and a lesser density interface at the bottom of the mixing zones in currently flooded Bahamian caves, produce optimal conditions where many bacteria thrive on the accumulated POC, POM, and DOC (Schwabe, 1999; Schwabe, 2002). The end-product of carbon metabolism by these microbes produces P_{CO2} levels of at least 3 to 4 times atmospheric concentration (Whitaker and Smart, 1997). We suggest that the resulting microbially-maintained acidic pH at these boundaries is responsible for the observed greater limestone dissolution that seems to have occurred at and around sea level (*sensu* Mylroie and Carew, 1988b), rather than the actual physical mixing of different water masses.

OTHER STUDIES

The role of bacteria in sulfuric acid speleogenesis (SAS) has become an accepted model for some cave development, such as large caves like Carlsbad and Lechuguilla in the Guadalupe Mountains of New Mexico (e.g., Hill, 1990), Lower Kane Cave in Wyoming (Engel et al., 2004), as well as others (e.g., Hose et al., 2000; Angert et al., 1998). Some work in the Bahamas has also indicated a role for sulphur-mediating bacteria (Bottrell et al., 1991; 1993); however, it is our contention that in the Bahamas, and similar carbonate settings, even traditional carbonic acid dissolution is also largely the result of bacterial activity. Whitaker and Smart (2006) suggested that CO_2 must be added to the ground water in the northern Bahamas by oxidation of surface- and soil-derived organics in the lens, but they did not document the presence of abundant populations of bacteria living in the rocks and groundwater as the probable source of CO_2. It is surprising that bacteria have not been recognized as an important aspect of limestone dissolution in the classical karst literature, because research in the 1930s demonstrated the existence of abundant and diverse bacteria on and within rock samples, and also documented CO_2 production associated with bacterial activity and the "decay of stone" (Paine et al., 1933).

Information on the abundance, distribution, and identification of CO_2-producing bacteria in the vadose zone of limestone in other localities is limited. However, information from the Black Creek-Middendorf-Cape Fear (BMC) aquifer system of South Carolina (Chapelle and Lovely, 1990), Patapsco aquifer system of southern Maryland (Chapelle et al., 1987), and the Madison aquifer system of the western United States (Chapelle and Lovely, 1990) indicate that bacterial activity, as measured by rates of CO_2 production, are in the 10^{-4} to 10^{-6} mmole per liter per year range--and all three of those systems are oligotrophic (Plummer et al., 1990). In comparison, the average CO_2 production from Altar Cave rock samples from San Salvador Island, Bahamas, and rock samples from Germany (Ehrlich, 1990) are substantially higher than those recorded from the BMC, Patapsco, and Maryland aquifers. Like the above-mentioned aquifer systems, lack of significant topsoil at the surface, and minor organic matter included within the rock matrix that encloses Altar Cave, San Salvador, also represents an oligotrophic environment. Under such nutrient-poor conditions, the presence of substantial populations of bacteria belonging to Order Actinomycetales is not surprising, as they are well-suited to growing in low-nutrient environments with alkaline pH (Lechevalier and Lechevalier, 1967; Barton et al., 2004).

Other investigators have also reported the dominance of *Actinomycetes* sp. in the rocks of limestone caves (Laiz et al., 1999; Cunningham et al., 1995; Groth et al., 1999). It was reported that in Altamira Cave located on the Cantabrian Cornice, Santillana del Mar, Spain, selective growth of *Actinomycetes* occurred on the cave wall sur-

faces (Laiz et al., 1999; Cunningham et al., 1995). Interestingly, in both the Bahamas and in Spain, analyses of drip waters demonstrated that the microbial communities in the water were different from those of the rocks themselves, and that the *Actinomycetes* remain in the rocks and are not liberated into the drip water.

METHODS

To enumerate bacteria from San Salvador drip water samples, 1 ml aliquots from each dripwater sample were aseptically transferred to 9 ml of sterile 0.9% v/w physiological saline and decimal dilution series were prepared. Tubes were vigorously vortexed between each serial transfer to ensure that the cells remained in suspension. Aliquots (0.1 ml) from each dilution were aseptically transferred to Tryptone Soy agar plates and spread over the plate using a sterile spreader. The plates were incubated at 25° C and inspected daily until no further colonies developed. The colonies on the plates were then counted.

To enumerate bacteria from San Salvador limestone samples, 1 g of limestone was weighed under sterile conditions and transferred to 9 ml sterile 0.9% v/w physiological saline solution. The limestone was crushed using a sterile stainless steel rod (10 mm diameter) until a fine suspension was formed. The limestone suspension was then subjected to 4 x 15 second bursts of sonication using a sterile MSE 150 soniprobe (MSE Instruments Ltd) to detach the bacterial cells. Decimal dilution series were prepared and the dilutions transferred onto half-strength agar plates and incubated in the same way as the drip water samples. The colonies on the plate were counted after no further development occurred.

To enumerate bacteria in formaldehyde-preserved water samples using DAPI staining, the procedure of Porter and Feig (1980) was used. Water samples (10 ml each) were filtered through 0.22 μm pore-size Nucleopore polycarbonate filters pre-stained with Irgalan Black. The bacteria were stained with DAPI (4'6 diamindio-2-phenylindole) at a final concentration of 2 $\mu g\ ml^{-1}$ for 10 minutes. After staining, the membranes were mounted on clean microscope slides with a drop of low-fluorescence immersion oil. The slides were examined using an Olympus BH-2 epifluorescence microscope at an excitation wavelength of 350 nm.

To quantify CO_2 production from rock samples, we used 20 ml serum vials that were sterilized along with tweezers, dental tools and rock chisels. Chisels were used to remove the hard surface sample and the soft samples at 2.5 cm deep into the wall were collected using a dental hook. Once in the serum vial, samples were sealed with a sterile butyl stopper and secured with an aluminum crimp. Two of the vials with rock samples were sterilized and the other samples were allowed to incubate for 14 days at 25° C. Using a sterile needle and 5 ml syringe, samples of air were removed from the serum vial and injected into GC carrier vials. The CO_2 analysis was run on a GOW-MAC Series 400 Gas Chromatograph (GC).

RESULTS AND DISCUSSION

Our microbial hypothesis is supported by a variety of data obtained from our recent study of rocks and water in the Bahamas, and from earlier studies (Schwabe et al., 1996; Schwabe 1999; Schwabe, 2002; Schwabe and Herbert, 2004). Rainwater collected under sterile conditions before contact with the ground on San Salvador Island, Bahamas in December 2005 contained ~10^3 bacterial cells per milliliter (Table 1). In contrast, water collected from dripstones in caves contained >10^4 to 10^5 cells/ml (Table 1), and limestone samples collected from Altar Cave on San Salvador Island, Bahamas, contained >10^6 viable cells per half gram of rock sample (Table 1).

The dominantly heterotrophic bacteria present in these limestone samples were aerobic Gram-positive bacteria identified as belonging to Order Actinomycetales (Figure 1; Table 2) that are known to produce CO_2 as an end-product of their carbon-based metabolism. In addition, bacteria recovered from 8-cm-deep rock cores into the wall of a flooded cave in the phreatic zone at 13.9, 14.0 and 15.9 m depths, had cell counts greater than the bacterial cell numbers recovered from the adjacent water column at equivalent

depths (Table 3) (Schwabe, 1999; Schwabe, 2002). In samples from rock cores recovered

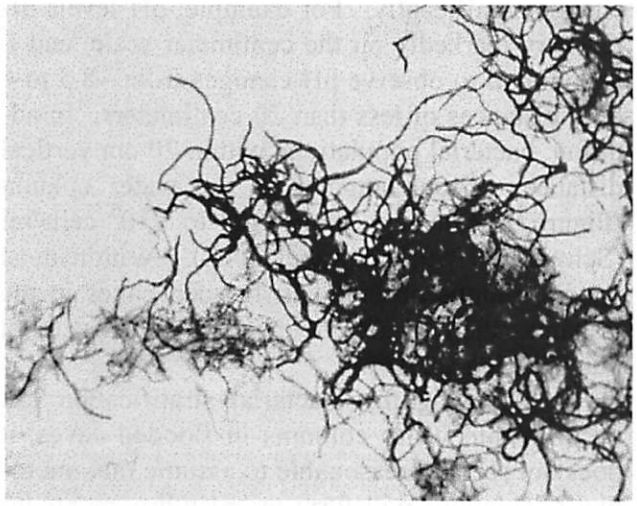

Figure 1. Photograph of bacteria of the Order Actinomycetales. Field of view is approximately 6 μm in width.

from the phreatic zone in Lucayan Caverns on Grand Bahama Island (Schwabe et al., 1996), bacterial counts ranged from 1.321 x 10^6 cells in the outer 2 cm, to 19,756 cells recorded 8 cm deep into the cave wall rock (Table 3). The rock core with the highest bacterial counts was from the top of the mixing zone. The presence of large microbial populations in the rock that comprise a number of different species, provides not only a significant potential for the production of CO_2, but also for other microbially-generated acids.

Furthermore, surface and 2.5-cm-deep cave-wall rock samples from the vadose zone in Altar Cave on San Salvador Island that were sealed in sterile vials for 14 days, yielded CO_2 contents ranging from 770 to 410 ppm above current atmospheric concentration (~380 ppm). In contrast, sterilized rock samples from the site yielded no excess CO_2. These data indicate that the indigenous bacteria present in the rock produce CO_2, and have the potential to sustain and drive CO_2-related dissolution processes in the vadose and phreatic zones (Figure 2). This suggests that the porosity and permeability of the limestone may be enhanced even when the rock is not saturated with water.

Additional evidence of the ability of bacteria to generate large quantities of CO_2 was observed by Schwabe when water samples were collected from the top of the freshwater/saltwater boundary of the water column of a vertical cave on South Andros Island, Bahamas (Schwabe, 1999; Schwabe, 2002). Within 6 hours of their collection, microbial generation of CO_2 (bacteria counts of >10^7 cells/ml) was so great that samples stored in 125 ml vials with ground-glass stoppers had the stoppers explosively expelled, even though the vials were refrigerated.

At other locations in the Bahamas, bacterial counts from water samples collected from the water column within flooded cave systems, reveal that the water column is not homogeneous with respect to numbers of bacteria (Schwabe et al., 1996; Schwabe, 1999; Schwabe, 2002; Schwabe and Herbert, 2004).

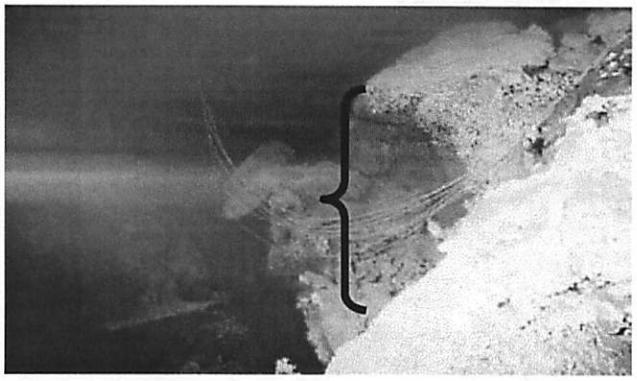

Figure 2. Banding within the water column and the mixing zone (MZ) in a cave on Grand Bahama Island, Bahamas. The bracket marks the MZ. Note the severely-etched rock within the bracket zone. In the water column to the left of the bracket, note the bands within the water column. Density differences support particles, including bacteria, copepods, and carbonate dust knocked off the ceiling by scuba exhaust. The water sampling tubes can be seen leading from the right upper corner of the photograph to where they are secured on a line attached from the ceiling of the cave to the floor.

Instead, bacteria often thrive in centimeter-thick zones (Figure 3) situated throughout the extent of the water column (Schwabe, 1999; Schwabe,

2002). These bands, or layers, are visibly darker than the intervening water (Figure 2), and reveal large populations of microscopic, photophobic, grey-black copepods of a species yet to be identified. Results from ^3H thymidine data indicates that there are large numbers of bacterial cells that are unaccounted for in those layers (Schwabe, 1999; Schwabe, 2002). We interpret these data as evidence that the large populations of copepods are grazing on the bacteria, thereby keeping their numbers low; and that both the copepods and the bacteria in such layers must produce abundant CO_2.

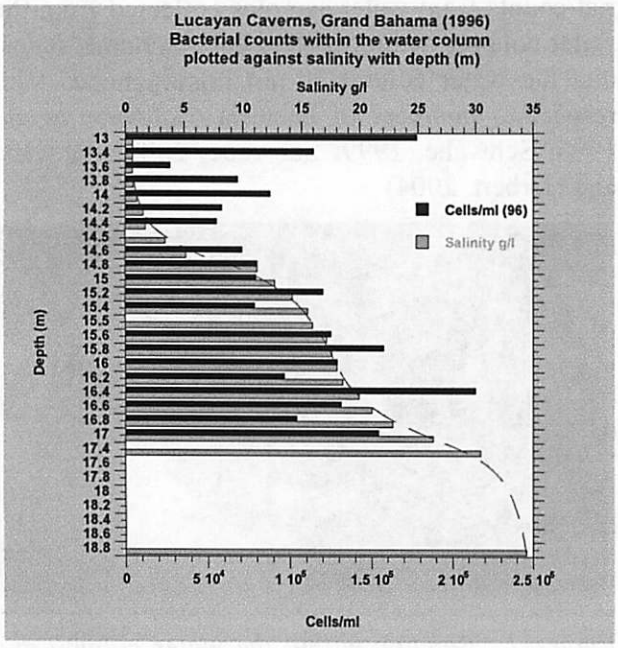

Figure 3. Graph of the salinity and corresponding bacterial counts through a water column in Lucayan Caverns, on Grand Bahama Island, Bahamas. The ceiling in the passage section represented here is at 13 m below sea level. The major density interface at the top of the mixing zone (MZ) begins at 14 m. A salinity step occurs at 16 m. In this particular passage, the water column reaches full marine salinity within the sediments on the floor at (~19.0 m).

The apparent zonation of bacteria in the water column of currently flooded caves in the Bahamas seems to be a result of varying densities within the water column (Figure 3). Geochemical profiles taken throughout the water column show that within a few centimeters, the general geochemical parameters and microbe counts often change significantly. For example, pH levels often vary markedly on the centimeter scale, and it is common to observe pH changes from ~8.5 to 4 over distances of less than 20 centimeters. In addition, bacterial populations within 20 cm vertical distances of one another in the water column (Figure 3) can vary from $<10^3$ to $>10^6$ cells/ml (Schwabe, 1999; Schwabe, 2002). Within most water columns observed in flooded caves in the Bahamas there is a coincidence of high bacterial numbers and acidic pH.

Knowing that bacterial stratification can occur within water columns in flooded caves, it does not seem unreasonable to assume that microbial populations will form microenvironments in the vadose zone of the rocks themselves, based on a discontinuous and variable supply of water, oxygen, and organics (Figure 4). Burial of organic material in the form of reefs, or subtidal grass/algal facies, or buried vegetation in eolianites may act as catalysts for void formation because they provide abundant sources of organic matter for interstitial bacteria. Microbial processes, whether in microenvironments or not, will affect the chemical composition of groundwater and the hydraulic properties of aquifers (Laiz et al., 1999). From the data obtained in our studies, we contend that contrary to the generally accepted model (White, 1988), the pH of rainwater does not play a significant role in carbonate dissolution, because the rainwater experiences significant buffering when it encounters the surface rocks (Figure 4). Evidence to support this conclusion was obtained by analysis of several samples of rainwater. Rainwater caught before contact with the ground had a pH of 5.72 (Table 1). In contrast, rainwater collected from profuse overflow from a building roof during a heavy rainstorm in February 2006 on San Salvador Island had a pH of 8.5, and analysis of the dissolved salts (Table 1) confirm that the pH reflected significant buffering from possible degassing and brief contact with the small quantity of $CaCO_3$ dust and rocks that are on the roof. Still further evidence was provided by analysis of rainwater that accumulated in

the catchment basin of the 18 acre concrete-covered hillside at the Gerace Research Centre during a large storm event in June 2006. The pH of the water collected about 18 hours after the rainstorm, was 9.18 (Jon Martin, pers. comm.). These data show that rainwater is thoroughly buffered within minutes to hours of contact with the surface.

In addition, analyses of water from open wells, cave drip water, brackish water, and seawater on San Salvador show that they are all supersaturated with respect to calcite, and predominantly at equilibrium with aragonite (Moore and Martin, 2006). Likewise, the calcite Saturation Index of some of our samples of water (Rain06, DR1, and Alt 1 [see Table 1]) indicate that the rainwater (Rain06, SI = +0.42) and drip water Alt1 (SI = +0.51) were supersaturated, and drip water DR1 (SI = -0.07) is saturated.

Table 1. Chemical and microbiological analyses of water and rock.

Sample	pH	T°C	Cl^- mg/l	HCO_3^- mg/l	Ca^{2+} mg/l	Mg^{2+} mg/l	Salinity g/l	Microbial counts
*DR0	**	**	**	**	**	**	**	6×10^3 cfu/ml
DR1	7.55	27.7	221	274	96	23	0.7	3.5×10^5 DC
Alt1	7.34	24.7	278	278	211	51	**	4.0×10^4 DC
Alt2	7.89	23.1	761	278	216	53	1.6	**
Rain05	**	**	**	**	**	**	**	1×10^3 DC
Rain06	8.54	24.0	15.6	310	6.9	0.9	0.1	**
Rain07	5.72	27.0	22.3	14	3.2	**	0.25	**
AltRk	**	**	**	**	**	**	**	$> 10^6$ cfu/0.5g

*Possible error on water analysis is ± 5%. *DR0 collected 12/04; DR1& Alt1 collected 12/29/05; Alt2 collected 01/05/06; rainwater collected 12/05, 02/06, and 01/07; AltRk collected 12/05. Under headings **indicates no data, cfu is colony-forming-units, DC is direct counts/ml using DAPI methods, DR is Dripping Rock, Alt, is Altar Cave, AltRk is Altar Cave wall rock samples.*

Table 2. Bacterial genera found in water samples from various sites.

Sample	Gram	Shape	Oxidase	Catalase	Genera
DR	-	Rods	+	+	*Sphingomonas*
DR	+	Cocci	-	+	*Micrococcus*
WBH	-	fat rods	-	+	*Flavobacterium*
WBH	-	short rods	+	+	*Sphingomonas*
WBH	+	short rods	-	+	*Microbacterium*
IW	-	rods	+wk	+	*Flavobacterium*
LHC	+	cocci	-	+	*Micrococcus*

DR-Dripping Rock, WBH-Watling's Blue Hole, IW- Ink Well Blue Hole, LHC - Lighthouse Cave.

Table 3. Bacterial counts within 2 cm sections of digested rock core from cave wall.

Depth m	Water	2.0 cm	4.0 cm	6.0 cm	8.0 cm
-13.9	68,077	737,904	479,843	144,045	32,945
-14.0	88,024	1,321,295	325,611	33,458	19,756
-15.9	157,326	510,504	193,642	75,787	23,291

Bacterial populations at 2 cm depth intervals into the wall rock of a cave show abundant populations at three water depths, and up to 8 cm deep into the rock. The major density interface between fresh and salt water is located at 14.0 m in the second chamber in Lucayan Caverns. The column headed "Water" shows bacteria counts from water samples collected adjacent to the cave wall where each rock core was taken. Note that bacteria are more abundant in the rock than the water up to at least 4 cm deep into the rock.

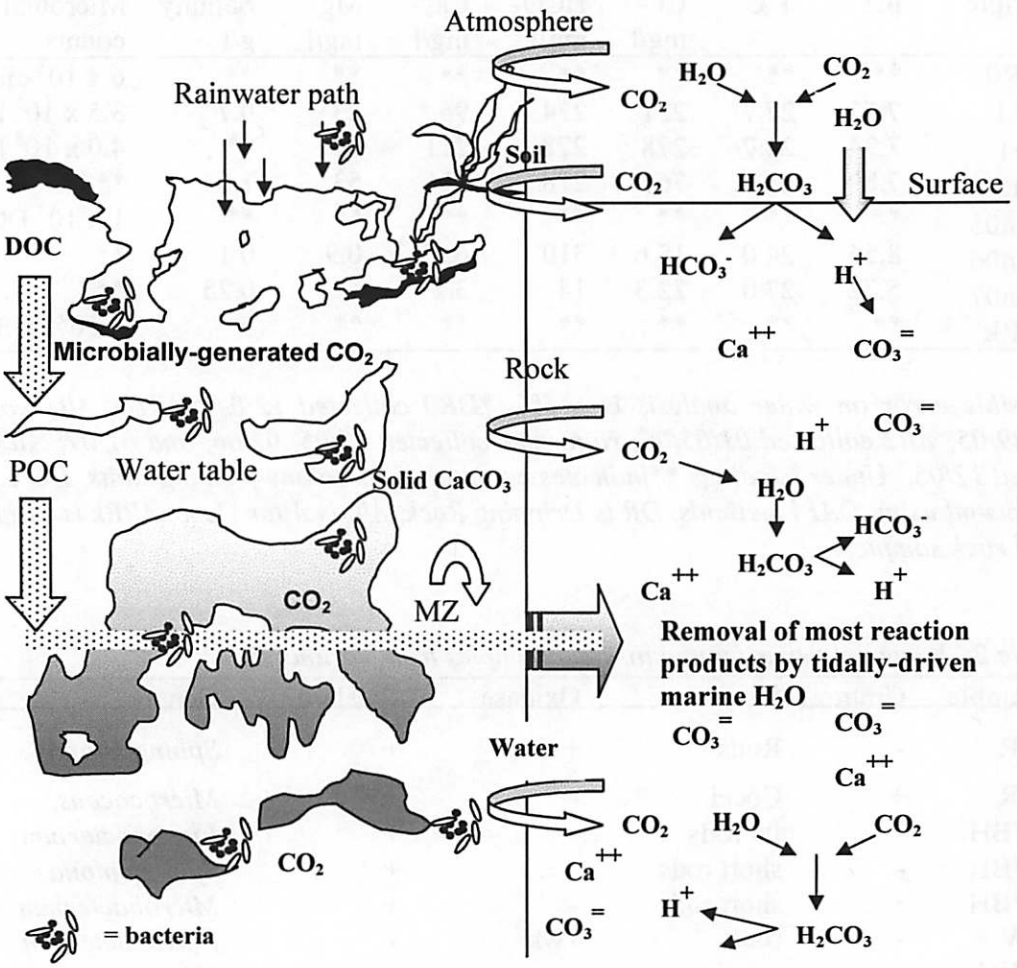

Figure 4. Schematic diagram of some of the chemical activities involved in the dissolution of $CaCO_3$ and the bacterial sources of CO_2 to drive it. Dark shading represents marine salinity, and White represents freshwater. MZ is the mixing zone. The diagram represents a rock column with a vadose and phreatic zone with water, gases, and bacteria.

CONCLUSIONS

It is generally agreed that dissolved carbon dioxide and other acids are the primary cause of the development of secondary porosity and permeability in limestones (White, 1988). However, we suggest that limestone dissolution in the Bahamas is not primarily the result of inorganic physico-chemical reactions and the initial acidic pH of rainwater. Instead, we suggest that rainwater is effectively buffered shortly after it contacts the ground; but as the water descends toward the water table, it is recharged with CO_2 that is produced as an end-product of carbon metabolism by the abundant indigenous bacterial flora living in the rock. As a result, dissolution may take place throughout the vadose zone, and sizable voids may develop in the vadose zone where the organic and moisture content of the rock is sufficient to support indigenous bacteria.

We further suggest that the portions of limestone strata in the phreatic zone, especially in the mixing zone and the upper marine section of the water column, are subjected to the greatest amount of water movement (which enhances solute removal) and the largest concentrations of bacteria (which produce abundant CO_2 and other acids). As a result, the dissolution potential of the water is greatest in those environments (Figure 2). Hence, caves develop to their greatest extent at or near sea level, which is consistent with the earlier-reported usefulness of flank margin caves as indicators of past sea-level position (Mylroie and Carew, 1988b). In addition, the recharging of vadose and phreatic ground water by microbially-derived CO_2 provides a reasonable explanation for how caves in these Bahamian rocks that have experienced only short episodes of exposure to freshwater and mixing zone water can be so large (Mylroie and Carew, 1988a). In addition, we suggest that it is likely that bacteria also control, or substantially contribute to, cave development in the vast majority of settings.

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