



Using coral holes to explore the historical ecology of Guam's coral reefs

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Abstract Push-coring is used to collect Holocene-aged coral sub-fossils, but its applications can be limited by underlying reef geology. Here, we report on a new approach of coring inundated coastal karst formations—i.e., coral holes—to determine the historical context of coral reefs in Guam. Three cores were extracted and processed to recover coral fragments as well as abundances of the photosymbiotic foraminifera *Baculogypsina sphaerulata*, a proxy for water clarity. Coral fragments, with the oldest dating to a median calibrated age of 221 cal. BP (1729 CE), revealed greater than 100 years of consistent accumulation and composition, suggesting a period of relative stability for macrobenthos. However, we documented a drop in *B. sphaerulata* abundance from approximately 100 years cal. BP, suggesting a period of environmental decline in Guam. Our results provide the first multi-centennial record of coral assemblages from Guam and provide a proof of concept for future historical investigations.

Keywords Coral reef · Historical ecology · Coral holes · *Baculogypsina sphaerulata* · *Acropora spp.*

Introduction

Historical analysis of coral reef communities can provide insights into ecological dynamics that span human time-scales (Pandolfi 2011) and can help alleviate the shifting baseline syndrome (Pauly 1995). Paleontological data, from coring efforts and studies of exposed facies, have revealed community structure and stability for millennia prior to rapid change over the last half century (McCulloch et al. 2003; Aronson et al. 2004). In many cases, this recent and rapid shift in the ecological state of corals reefs has resulted from the increased human influence on the environment (Jackson 1997).

Push-coring through unconsolidated coral reef framework is a popular method to obtain Holocene reef fossils given its wide applicability, efficiency, and low environmental impact

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(Dardeau et al. 2000; Aronson et al. 2002). Yet, unconsolidated reef matrices are scarce on many carbonate islands. For instance, although corals are abundant on the nearshore reefs of Guam, the largest island in Micronesia, the local geology consists mainly of basement rock covered with a thin layer (<0.5 m) of marine sediment. Moreover, there are no known raised or inundated fossil reefs from previous sea-level high stands, making the Holocene history of Guam's coral reefs challenging to study.

However, in several locations the Pliocene–Pleistocene basement limestone features karst dissolution caves, or “coral holes,” which formed during previous glacial maximums. These coral holes, which occur behind the reef crest, can be discerned in satellite images by their discrete shapes and lighter colorations among patches of coral and hard bottom (Fig. 1; Burdick 2005). Since these holes trap sediment, live coral, and rubble from the surrounding reef, they might offer a way to reconstruct reef community histories in this region.

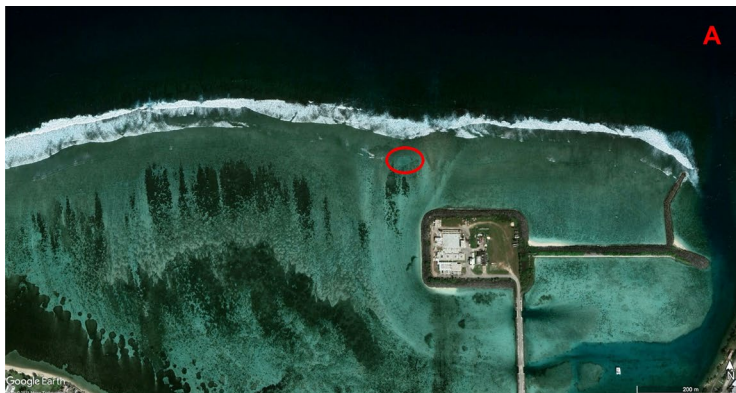
Included within these reef sediments are assemblages of symbiont-bearing foraminifera. Many species are sensitive to nutrient loading (Hallock 1981, 2000; Zamora-Duran et al. 2020), making foraminifera useful proxies of environmental change associated with nutrient pollution (Barmawidjaja et al. 1995; Carnahan et al. 2009). This idea has

been applied to coral reef studies with the establishment of the FORAM Index (Hallock et al. 2003), which quantifies reef viability based on the relative abundances of different foraminifera groups. According to this index, areas that support the healthiest reefs are characterized by having a large abundance of photosymbiotic foraminifera, which thrive in oligotrophic waters.

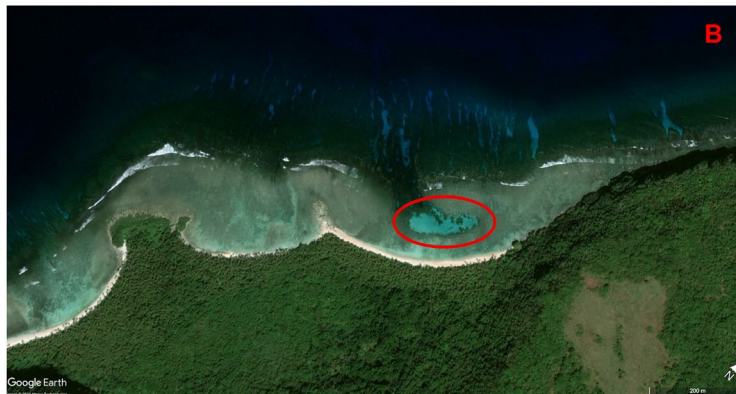
Like other reefs in the North Pacific, the vitality of Guam's coral reefs has been declining over the last 40 years (Burdick et al. 2008; Andrew et al. 2011), though the full extent of loss is difficult to establish without a pre-anthropogenic baseline. Recent threats to reefs include declining water quality from development, jungle burning-induced sedimentation (Wolanski et al. 2003; Williams et al. 2015), sewage outflow from inadequate treatment plants (Redding et al. 2013; Pinkerton et al. 2015; Duprey et al. 2017), increased outbreaks of coral predators such as crown-of-thorns sea star *Acanthaster planci* (COTS; Colgan 1987), overfishing (Houk et al. 2012; Bejarano et al. 2013), and coral diseases (Redding et al. 2013). Additionally, Guam's reefs have not escaped global threats such as climate change and thermal bleaching. Between 2013 and 2017, bleaching events led to the loss of approximately 30–60% of coral cover on reefs around the island (Raymundo et al. 2019). *Acropora* spp. were particularly impacted, with a documented loss of

Fig. 1 Study area, Guam. **A** Location of West Hagåtña (Agaña) Bay and the coral hole cored (red oval). **B** Location of Shark's Hole, another coral hole cored and referenced in the manuscript, although data not presented. Panel B was included to show the distinction in the coral holes from the surrounding reef framework via satellite imagery. Imagery obtained from Google Earth Pro on August 30, 2023

East Agana Bay, 2015



Sharks Hole, 2015



over 36% due to their highly sensitive biology (Raymundo et al. 2019), a collapse mirrored on a global scale (Renema et al. 2016). Though these threats reduced coral cover, less is known about changes in community structure, particularly over the Guam's longer-term history.

Here, we present the first known historical record of coral biodiversity in Guam over the last two hundred and eighty years. We employ a sediment push-coring method to collect coral sub-fossil data from karst-formed coral holes. We also present a record of changes in relative abundance of *Baculogypsina sphaerulata*, a photosymbiotic foraminifer that thrives in oligotrophic waters, as a proxy for water clarity. This study offers a proof-of-concept for documenting historical changes in coral diversity on reefs that lack significant reef matrix substrate.

Materials and methods

Guam is the southernmost island of the Mariana Islands chain, located in the Micronesia sub-region of Oceania in the western Pacific. Manual push-cores ($n=3$) were taken from a coral hole (approx. 20×40 m wide and 0.5 m below the height of the surrounding reef) located in West Hagåtña (Agaña) Bay (13.48244 N, 144.7463 E) on the western coast of Guam (Fig. 1; Burdick 2005). Cores (AG-1, AG-2 and AG-3) were taken at 5 m intervals across the hole using an open-barrel coring technique (Dardeau et al. 2000; Aronson et al. 2002). A galvanized steel tube (2.5 m length \times 6.35 cm diameter) was driven into the coral hole, capped at the top, extracted from the sediment and rubble matrix, and immediately capped at the bottom to retain the internal sediment structure. Cores were then extruded into 5 cm segments at the University of Guam's marine laboratory. Sediment samples were dried at 80 °C and weighed to determine dry weight per core segment. Each segment was sifted using an 8000, 1000, and 500 μm mesh soil sifters. Coral fragments from the $> 8000 \mu\text{m}$ fraction were identified to family and all coral materials from the $> 1000 \mu\text{m}$ fraction were weighed to determine total coral abundance per 5 cm segment. Corals were identified using a published coral atlas (Veron 2000), compared to field photographs of coral from Guam, or referred to coral taxonomists expert in the regional fauna. Foraminifera counts were made from 4 g subsamples of the same core segments that corals were analyzed, using a sediment splitter from the $> 500 \mu\text{m}$ fraction of AG-1 and AG-2 cores. Each sample was washed with deionized water over a 63- μm sieve, air-dried on filter paper, and then counted in triplicate.

For a given segment, fragments from each coral family were weighed, converted to proportional abundance to assess community composition of the surrounding reef, and total coral weight was calculated. Coral fragments from the

deepest segment of all cores and one sample from the middle segment of AG-2 and AG-3 were radiocarbon-dated at the National Ocean Sciences Accelerator Mass Spectrometry Facility at Woods Hole Oceanographic Institution (Massachusetts, USA). Coral fragments chosen for radiocarbon dating were well-preserved and showed no signs of diagenesis externally (i.e., severe encrustation, pitting, biotic boring, abiotic weather) or when cut-open. The top segment of each core was assumed to correspond to the collection year (2015) since cores were taken through recently fragmented, yet living coral rubble found at the top of the coral hole.

Radiocarbon ages were calibrated using the Marine20 curve (Heaton et al. 2020), and age–depth models were calculated using Bayesian modeling in OxCal version 4.4 (Ramsey 2009). The ΔR value used to calibrate coral samples was -141 ± 50 (Southon et al. 2002), retrieved from CALIB (calib.org). The additional ΔR (-14 ± 50) reported for Guam was not included for analysis because it was sampled from a mobile marine gastropod (*Gibberulus gibberulus*: Linnaeus, 1758) with a different life history than a sessile coral, meaning its carbon assimilation sources would be different. Additionally, the gastropod's ΔR was an order of magnitude different than the next eight closest available ΔR dates for the region. A P-sequence model was used in OxCal with a variable k -value (Ramsey and Lee 2013). This model allowed for the incorporation of depth and sequence data (P-sequence) from our cores and accounted for variable sedimentation rates (variable k -values). Ages are reported in both calibrated years before present (cal. BP) and calendar years CE.

Total percent coral abundances (g), coral community composition (relative abundance by family), and foraminifera abundances (per 4 g sub-sample, corrected by the time each 5 cm segment encompasses) were analyzed against core segment age to determine temporal variation. Then, z-scores were calculated to compare total coral abundance and foraminifera abundance to allow for comparative analysis. Z-score data were combined by time, and a nonparametric Loess smooth curve was fit to identify composition trends using the ggplot2 package and *geom_smooth* function (Wickham 2016). The span chosen for corals and foraminifera (0.55, 0.60, respectively) for the LOESS smooth function that generated the least error was determined by generalized cross validation (Takezawa 2005). Analyses were performed in RStudio, version 2022.02.3 (R Core Team 2022).

Results and discussion

All cores contained coral fragments in most segments, embedded within a gravelly, muddy matrix. On average, each 5 cm layer contained 40.5 ± 37.8 g of coral and accounted for $20.7 \pm 17.9\%$ of total fragment weight. *Baculogypsina*

sphaerulata was the dominant foraminifera species found in all cores. *Acropora* spp. fragments from bottom segments of the three cores dated to approximately 104, 143, 221 cal. BP, or 1848, 1807, and 1729 CE (Table 1).

Taxonomically, 99% of coral fragments from the cores belonged to four families: Acroporidae, Pocilloporidae, Faviidae, and Poritidae. Acroporidae was the most abundant coral family in cores AG-1 and AG-3 for ~200-years; whereas, Pocilloporidae was most abundant in core AG-2. In all cores, Pocilloporidae abundance was variable and was often inversely related to Acroporidae. Over the last 50 years in AG-1 and AG-2 Pocilloporidae and/or Poritidae increased in relative dominance (Fig. 2). This shift is consistent with community patterns documented elsewhere (Greenstein et al. 1998), including in Guam (Raymundo et al. 2019; Greene et al. 2020). One possible explanation for this pattern of decreasing Acroporid abundance is their life-history strategy. Acroporids tend to be highly competitive and fast growing, making them prominent reef developers; however, they are also highly sensitive to environmental change (Darling et al. 2012) which has led to their recent global

decline (Renema et al. 2016; Cramer et al. 2020; Cybulski et al. 2020). The compiled core record (Figs. 1 and 2) could be documenting the decline of sensitive coral groups such as Acroporids, previously seen in nearby Guamanian reefs from COTS outbreaks (Colgan 1987) and bleaching (Raymundo et al. 2019). Alternatively, some of the variability in coral relative abundance (Fig. 1) could be a result of how the coral rubble is deposited in the coral hole. Deposition of coral sub-fossils into coral holes is likely less uniform than the accumulation of reef matrix layers, the typical substrate sampled using push-cores. However, even if this pattern is taphonomic and driven by variable sedimentation, it is still indicative of changes in environmental conditions that led to decreased instances of Acroporid deposition.

Starting at approximately 1865 CE, we documented a sharp decline in *B. sphaerulata* z-scores (Fig. 3). Such a severe decline, with a lag in coral abundance and taxonomic changes (Figs. 2 and 3) suggests one or multiple stressors that impacted each taxon differently. The drop in *B. sphaerulata* could be linked to a loss of habitat, or water clarity declines driven by increased nutrients and/or

Table 1 Radiocarbon results from AMS radiocarbon dating at Woods Hole Oceanographic Institution (Massachusetts, USA). Median calibrated ages were then converted to calendar years CE for plotting

Core	Depth (cm)	F-modern	^{14}C Age	^{14}C error	$\Delta^{14}\text{C}$	Calibrated age, BP	Calendar year, CE	1σ error
AG-1	105	0.95650	355	15	-50.94	143	1807	42
AG-2	120	0.96030	325	15	-47.21	104	1848	48
AG-2	60	0.97560	200	20	-32.09	21	1929	23
AG-3	60	0.93140	570	15	-75.85	221	1729	80
AG-3	30	0.98140	150	15	-26.26	54	1896	35

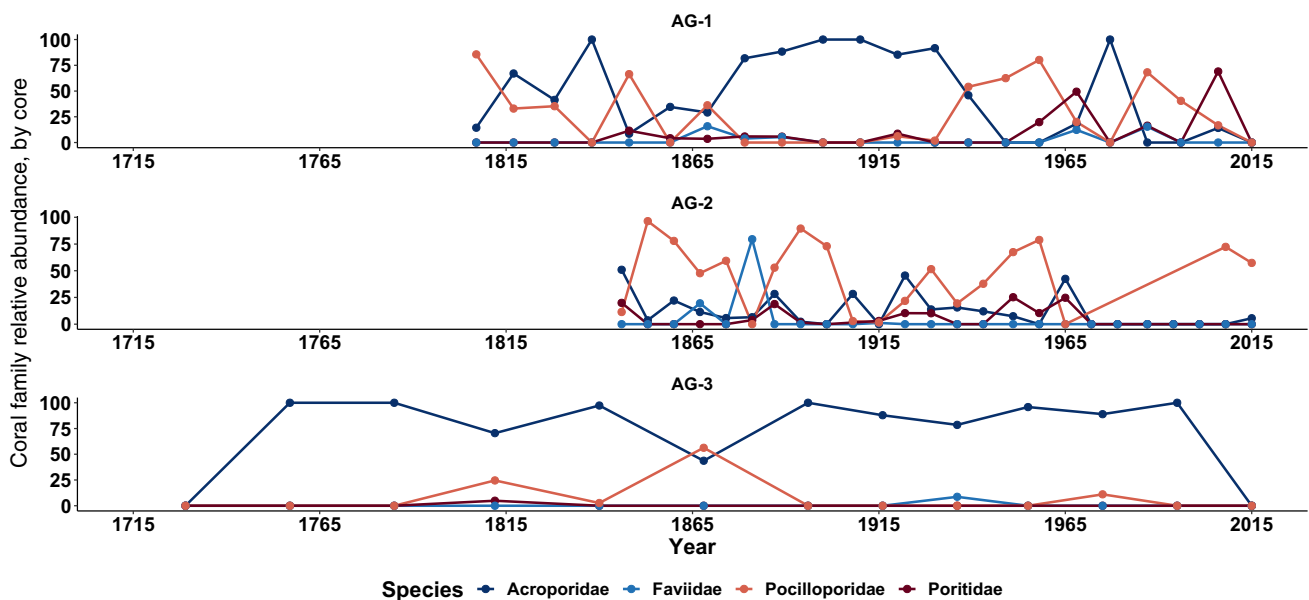


Fig. 2 Coral relative abundances, split by family, by core. Sections that do not add up to 100% represent unidentified coral sub-fossils

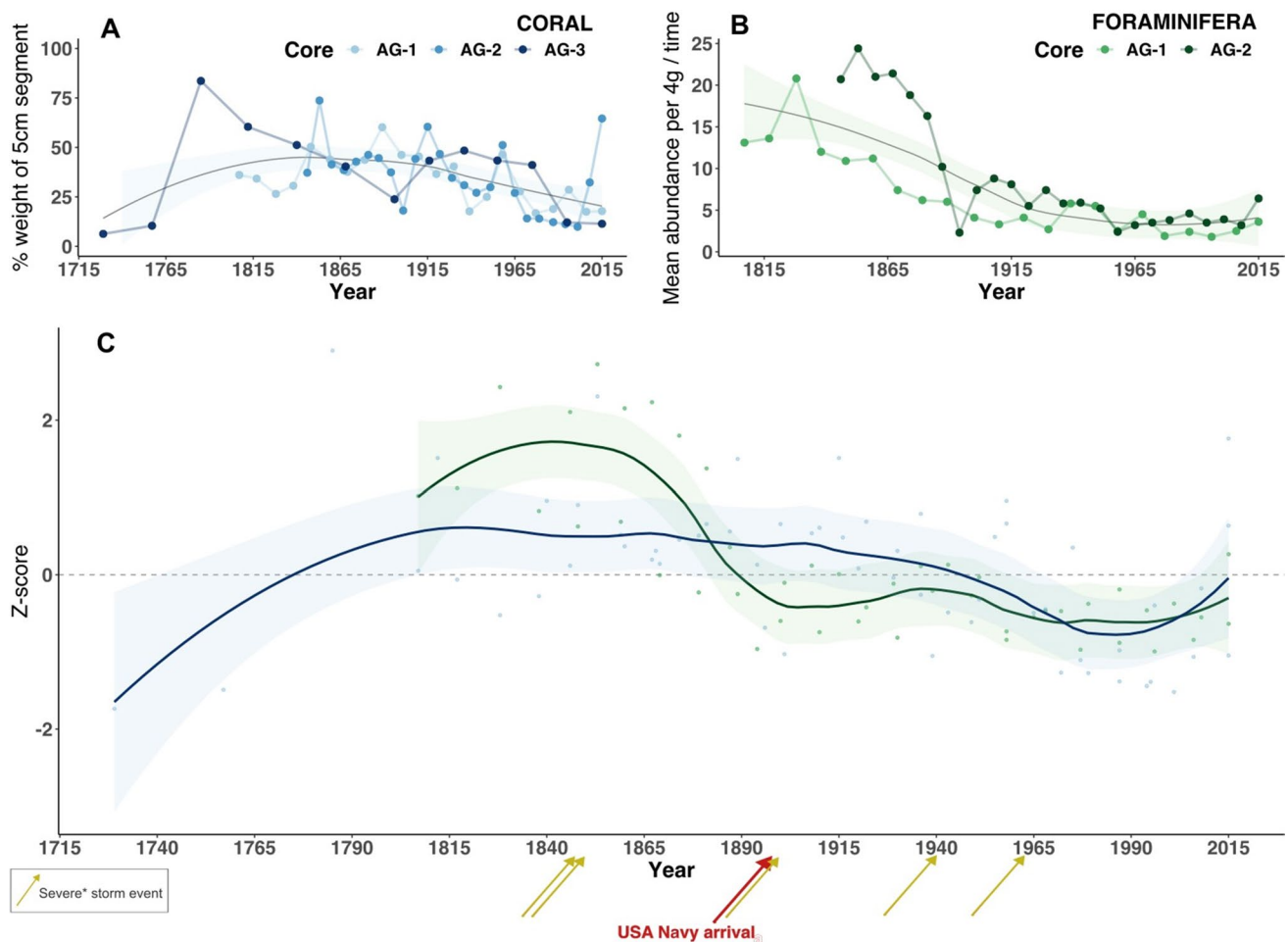


Fig. 3 Core summaries. **A** Total percent weight of coral fragments in the $>1000\ \mu\text{m}$ sieve fraction, by core; and **B** average *Baculogypsina sphaerulata* counts by 4 g sediment sample, corrected by time by dividing the total number by the years represented in the 5 cm core segment. All data were fitted with a LOESS smooth with a span of 0.95. Panel C shows both data sets converted to z-scores, and then

LOESS smoothed separately with a span of 0.55 and 0.60 chosen for corals and *B. sphaerulata*, respectively. Significant events in Guam's history are highlighted by arrows. "Severe Storms" are those labeled as such and documented to have caused extreme damage and loss of life in Carano and Sanchez (1964)

sedimentation (Hallock 1981, 2000). Storm-related deteriorations to suitable habitat for *B. sphaerulata*, followed by the additional anthropogenic stressors from human development could be one explanation to the decline and subsequent stagnation of our foraminifera record. For example, although the timing based on our current age model is not exact a possible cause in abundance declines could have been two severe storms that were documented on the island in 1848 and 1849 CE (Carano 1964). The fact that the foraminifera abundance remains low after the storm events with no recovery suggests that this decline was not due to the storms directly, or at least not the storms alone. The arrival of the US Navy in 1899 CE increased the population fivefold from $\sim 10,000$ to $\sim 50,000$ in 50 years. This sparked coastal development around nearby Hagåtña—the original capital (Bayman and Peterson 2016), likely

deteriorating water quality and clarity. This would have been detrimental to *B. sphaerulata* recovery.

The gradual decrease in coral abundance might indicate initial resilience to factors that caused the severe *B. sphaerulata* decline. However, sediment loading and added nutrients often associated with terrestrial runoff from coastal development (Fabricius 2005) as well as repeated intense storms between 1900 and 1965 CE (Scoffin 1993) could have been what caused the more drastic coral declines starting around 1915 CE (Fig. 3). Similar impacts from acute storm events and increased population and development resulted in widespread *Acropora* mortality on the inshore Great Barrier Reef (Roff et al. 2013).

Alternatively, it is possible that our abundance declines are not environmental or anthropogenic, but either taphonomic or an artifact of age model uncertainty. These holes

could have rapidly filled after Holocene sea-level rise, resulting in repeated replacement and time-averaging of its top portion. However, because of the linear age progression of the dates, this is unlikely. A more parsimonious interpretation is that the coral reef accreted enough around the hole to create more headspace for debris accumulation. Additionally, the wide variation in our dates (between ± 23 and 80 years) makes associating specific events to declines in corals and foraminifera difficult. Additional coring and dating are needed to strengthen links between environmental and biotic changes.

Regardless, our top and bottom dates offer a snapshot of past coral communities and foraminifera assemblages in Guam for over 280 years. We show clear declines in both foraminifera and coral abundances, although timings of these declines vary, and the direct causes are unclear. This method could be expanded to other known coral holes around Guam such as Shark's Hole (Fig. 1; 13.558630 N, 144.815933 E, approx. 145 \times 45 m wide) and Agat Bay (13.372192 N, 144.647095 E approx. 80 \times 40 m wide; Burdick 2005) which are known to accumulate coral fragments, or other Pleistocene karst-formed reef islands that are difficult to core such as Okinawa or Dongsha Atoll.

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Data availability All data needed to complete the analyses in this manuscript will be available on a GitHub repository after publication.

Declarations

Conflict of interest The authors report no conflicts of interest.

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