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Key Points:

- Reef condition at two emergent fossil reticulate reefs in Kiribati was reconstructed using paleoecological surveys and radiometric dating
- Temporally distinct episodes of reef growth, followed by reef shutdown, were observed through the late Holocene
- Reef shutdown was likely associated with storm-deposited ridges on the atoll rim, driving changes in lagoon water, restricting coral growth

Supporting Information:

Supporting Information may be found in the online version of this article.

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Fossil Reefs Reveal Temporally Distinct Late Holocene Lagoonal Reef Shutdown Episodes at Kiritimati Island, Central Pacific

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Abstract An extremely rare example of well-preserved emergent Holocene fossil reefs exists at Kiritimati Island, central Pacific. Fossil reefs are rich geological archives of paleoenvironmental change. The first paleoecological surveys of two fossil reefs are presented, revealing high coral cover (40–50%) and low diversity (6 genera). Fossil coral ages suggest reefs exhibited disparity in the timing of reef development (4,113 and 1,915 cal yBP) and ecological surveys show different coral compositions (*Acropora* or *Porites* dominant), between reefs. Results constrain two discrete episodes of reef shutdown (at 2,905 and 1,705 cal yBP) as lagoonal reefs thrived, and subsequently died off, through the late Holocene. Shifts in physio-chemical conditions associated with reduced lagoon flushing following storm-driven changes in atoll rim morphology are argued as the driver for the staged reef die-off. The findings have implications for interpreting past and future eco-morphological change on atolls, given projected increases in storminess with climate change.

Plain Language Summary Fossil coral reefs include the skeletal remains of corals and are rarely preserved in good condition above modern sea level. Such reefs are rich archives that hold information about past environmental and ecological conditions at the time of reef development. A rare and expansive example of fossil reefs grew during the period 7,000 to 1,000 years ago at Kiritimati Island, Kiribati. Surveys and radiometric dating were used to reveal, for the first time, the age, elevation, and coral ecology of two of the most well-preserved fossil reefs on Kiritimati Island (between 4,000 and 2,000 years ago). Results show that the reefs flourished during different time periods and were dominated by different coral taxa, before dying off. We argue that reef die-off is attributed to changing lagoon seawater conditions that became intolerable for coral growth. These changing water conditions were the result of storm-induced changes at the atoll rim that enclosed the lagoon and reduced flushing. As tropical cyclones are projected to increase in frequency and severity under global climate change, our results are critical for understanding the future responses of mid-oceanic atolls and their supporting ecologies.

1. Introduction

Atoll morphology reflects the interplay of: (a) glacio-eustatic sea-level change involving karstification processes during glacial lowstands and reef growth during periods of sea-level rise; (b) reef hydrodynamics, biological production, and sediment transport processes during sea-level highstands (Dickinson, 2004; Purdy & Winterer, 2001); and (c) storm-driven sediment accumulation (Baines & McLean, 1976; Kench et al., 2018). Atolls can be characterized into different morphological evolutionary stages (McLean & Woodroffe, 1994) from early stage “empty bucket” atolls with narrow reef rims enclosing a deep central lagoon, through to mature-stage “filled-bucket” atolls with complete sediment-filled lagoons (Purdy & Gischler, 2005). Reticulate atolls represent an intermediate stage characterized by interconnecting reefs forming a “honey-comb” pattern (Guilcher, 1988), that is either inherited from underlying karst topography (Purdy, 1974), or formed through constructional processes (Schlager & Purkis, 2013). While biophysical conditions within these semienclosed or closed lagoons differ from open atoll lagoons, they can support coral communities (Barott et al., 2010; Camp et al., 2019; Delesalle, 1985). These coral communities are sensitive to shifts in environmental conditions associated with changes in lagoon circulation, sea-level fall, changes in the wave climate,

increased turbidity and sedimentation, and elevated ocean temperature or salinity. Such changes may transition reef communities toward stress-tolerant taxa (Burt et al., 2020; Guinotte et al., 2003), or result in mass mortality as lagoons rapidly become no longer viable for coral growth (Delesalle, 1985).

Fossil coral reefs are geological archives of past reef communities, and together with radiometric dating and paleoecological reconstructions, can be used to infer prior reef conditions (e.g., turbidity, temperature, water level, and hydrodynamics). Reef cores that extend through Holocene reef sequences are often used to obtain records of paleoecological composition and change (Johnson et al., 2017; Montaggioni, 2005; Ryan et al., 2018). However, spatial interpretations of these data are limited as cores provide only a snapshot of coral communities, equivalent to the diameter of the core barrel (7–11 cm) and may not capture broader-scale ecological patterns and less abundant taxa. In contrast, well-preserved emergent reefs offer an opportunity to explore past three-dimensional reefscape and develop high-resolution spatial data sets of reef communities using similar methods as for contemporary reef ecology. Emergent well-preserved fossil coral reefs, such as those presented here, are globally rare, requiring a prolonged relative sea-level highstand to develop and suitable conditions for preservation, including appropriate isolation from human activities and environmental settings that minimize diagenetic alteration and/or erosion.

Here, we provide the first paleoecological surveys of emergent fossil reefs in the central Pacific, for two expansive and well-preserved reef sites on Kiritimati (Christmas) Island, Republic of Kiribati. Kiritimati Island is a partially filled-bucket atoll (Purdy & Gischler, 2005) with the atoll interior characterized by a reticulate network of fossil reefs (McGregor et al., 2011; Woodroffe & McLean, 1998) that impound >500 brackish to hypersaline lakes (Saenger et al., 2006; Schmitt et al., 2019; Valencia, 1977). The excellent preservation of Holocene reefs at Kiritimati Island provides paleo-coral community context to infer geomorphic and physio-chemical changes in the reticulate lagoon system. This is particularly important given the prominence of Kiritimati Island in paleoclimate reconstructions (Cobb et al., 2013; Grothe et al., 2020; Woodroffe & Gagan, 2000). To date, existing age data from interior fossil microatolls of Kiritimati Island show no clear spatial-age pattern (McGregor et al., 2011; Woodroffe et al., 2012) and are therefore inconclusive regarding the timing and nature of reticulate lagoonal reef growth and shutdown. Our findings present new spatiotemporal constraints on late Holocene changes in lagoon biophysical conditions consistent with discreet episodes of reticulate lagoon shutdown.

2. Materials and Methods

Benthic cover and community composition were quantified at two emergent fossil reefs located at Lake 122 (Skeleton Reef: SR) and 5 km away at Lake 125 (Tenei Rababa, referred to as Ghost Reef: GR) within the interior of Kiritimati Island (Figure 1, see supporting information for a description of the study location). Point-intercept surveys were conducted across the entire section of exposed reef at five randomly established cross-reef transects at each site (spaced ~50–100 m apart). Transects varied in length between reefs (14.2–27.1 m at SR and 15.0–24.6 m at GR) and were determined by local reef morphology, as they ran from the upper extent of the exposed reef near the vegetation line to the contemporary lakeshore/waters edge (Figures 1, 2, and S7). Benthic cover (i.e., sediment substrate, coral rubble, fossil coral, mollusks) directly beneath each transect line was recorded at 10-cm intervals (total of 2,049 points). A photographic biodiversity survey was completed at each site, whereby all coral genera observed during a roaming survey of the area between transects were photographed and identified. The biodiversity surveys confirmed our point-intercept surveys were representative of the overall reef coral composition. *In situ* fossil coral ($n = 23$) and mollusk ($n = 1$, *Tridacna* sp.) samples were collected from along the transects on the upper reef surface and dated by Accelerator Mass Spectrometry (AMS) radiocarbon (^{14}C) dating (Table S1). Topographic elevation of each fossil reef transect was determined using a Trimble Real Time Kinematic Geographic Positioning System (RTK GPS). Details of sample preparation for dating and elevation data processing are presented in the supporting information. Statistical analyses (nonparametric multidimensional scaling, SIMPER, Kruskal-Wallis tests and post-hoc pair-wise Mann-Whitney U tests) were performed on the fossil reef ecological and elevation data to explore interreef and intrareef flat variability in benthic composition and elevation (see supporting information). Nonparametric statistics were used as parametric assumptions (normally distributed data) were not met. In the absence of known and/or extensive reef development within the contemporary lagoon, we surveyed the modern reef flat at Cecile Peninsula (Figure 1) using the

Figure 1. Location of (a) study sites on Kiritimati Island, and transect locations at (b) Ghost Reef: GR (Tenei Rababa) and (c) Skeleton Reef: SR (Lake 122).

Figure 2. Cross-sectional profiles for (a) Ghost Reef (GR-T1) and (b) Skeleton Reef (SR-T1), where 0 = 20.0 m above WGS84 ellipsoid. Profiles for remaining transects are presented in Figure S7. Photographs of the characteristic coral composition and cover at each fossil reef site are presented in (c) (GR—massive *Porites* spp. dominated), (d) microatoll morphology, and (e) (SR—branching *Acropora* spp. dominated).

Figure 3. Benthic cover of reef taxa. (a) Site-averaged contribution of reef taxa at Ghost Reef (GR) and Skeleton Reef (SR). (b) Reef taxa recorded at each transect within each site. “Other” represents *Fungia* spp. and oysters.

same point-intercept method as at the fossil reef sites to provide a modern ecological analogue (supporting information). While the modern reef flat provides the best available analogue, it is important to recognize that the hydrodynamic conditions were likely very different inside the sheltered palaeo-lagoon, compared to the higher energy reef flat at the leeward atoll rim.

3. Results

3.1. Composition of Fossil Reefs

Fossil coral assemblages were characterized by high relative abundance of coral and low diversity (six identified coral genera). Benthic cover of corals across transects averaged $50 \pm 12\%$ (mean ± 1 standard deviation) at GR and $40 \pm 9\%$ at SR (Figure 3 and Table S2). Four dominant genera were recorded in benthic surveys: massive *Porites* spp. (typically microatoll morphology between 3.0 and 4.0 m in diameter), branching and tabular *Acropora* spp., massive *Dipsastraea* spp., and free-living *Fungia* spp. Other massive coral genera (e.g., *Platygyra* and *Goniastrea*) were observed, however, poor corallite preservation made identification difficult in some instances. Some weathered, unidentifiable corals (massive and branching) were found in the photographic biodiversity surveys that were likely not one of the recorded genera; however, they were rare. Remaining substrates were sand/gravel (averaging $17.3 \pm 8.3\%$ and $24.1 \pm 8.8\%$ at GR and SR, respectively) and a cemented detrital sediment cap (averaging $24.8 \pm 14.6\%$ and $18.9 \pm 5.6\%$ at GR and SR, respectively) (Table S2 and Figure S1), with minor contributions of coral rubble, mollusks (including *Tridacna* spp., and oysters) and coralline algae in articulated and rhodolith form (Figures 3, S1, S5, and Table S2). While the contributions of mollusks and coralline algae to benthic surveys were minor ($<4\%$ and $<2\%$ on average at GR and SR, respectively, Table S2), the abundance of well-preserved, in situ *Tridacna* spp. was notable at both reefs. Disarticulated rhodoliths were common at GR (Figure S5), but rarely found at SR.

An ordination of fossil reef community data shows separation between the two fossil reef sites, except for transect SR-T2 (Figure S3). The two sites (SR and GR) were comprised of significantly different coral communities (PERMANOVA: $F_{1,8} = 8.464$, $p = 0.0461$). The variance between sites is largely due to the higher proportion of massive *Porites* spp. at GR (averaging $42.6 \pm 16.3\%$ of total benthic cover) compared to SR ($10.6 \pm 23.6\%$) and a higher proportion of branching *Acropora* spp. observed at SR (averaging $27.8 \pm 16.4\%$ of total benthic cover) compared to GR ($4.2 \pm 3.1\%$) (Figure 3 and Table S2). Results from SIMPER analysis confirm that collectively, these two taxa were responsible for 86.4% of interreef dissimilarity (Table S3). Tabular *Acropora* spp. were only recorded at SR in low abundance (averaging $0.7 \pm 1.6\%$ of total benthic cover), while *Fungia* spp. were only recorded at GR and averaged $0.1 \pm 0.2\%$ of total benthic cover (Table S2).

Figure 4. Interpreted biophysical changes within Kiritimati lagoon through time based on coral community composition and reef elevation. Time is shown as thousands of years before present (K yBP). Published data to support biophysical changes are shown by numbers (1) Woodroffe et al., 2012 and (2) Grothe et al., 2016.

3.2. Age and Elevation of Fossil Reefs

Radiometric dating of coral samples defines two distinct age cohorts, with ages at SR ranging from 4,113 to 2,905 calibrated years before present, where present is 1950 CE (cal yBP), and ages from GR between 1,915 and 1,705 cal yBP (except for one outlier at 3,482 cal yBP) (Table S1). Consequently, SR is ~1,500 years older and flourished for a longer duration (~1,200 years) than GR (~200 years). Despite marked differences in age, both reefs formed within a similar elevation zone, between 0.5 and 2.0 m above the lowest tidal level at Kiritimati Island observed by Woodroffe et al. (2012) (Figures 2, S6, and S7). At SR the higher elevation sites are older, with coral samples becoming younger with proximity to the modern lakeshore (Figure S6). This pattern is not as pronounced at GR, which may be a function of the age and elevation data often representing the upper surfaces of slow-growing massive *Porites* spp. corals, rather than the reef flat surface. Results from Kruskal-Wallis tests identify significant differences in elevation between different coral genera at SR ($n = 5$; Chi-square = 45, $p \leq 0.005$), but not GR ($n = 4$; Chi-square = 7.89, $p = 0.484$) (Table S4a). Results from post-hoc Mann-Whitney U tests were used to identify differences in coral genera with elevation at SR (Table S4c) and show a significant difference in elevation (~50 cm on average) between branching *Acropora* spp. and massive *Porites* spp. corals (Table S4c).

4. Discussion and Conclusions

Our analyses of the fossil reefs on Kiritimati Island reveal distinct differences in ecological composition and age, and provide new insights into changes in the morphology, ecology and related hydrodynamic regimes during the late Holocene. The 1,000-years hiatus between reef ages at SR and GR (between 2,905 and 1,915 cal yBP) suggests these two reefs flourished at discrete time periods (Figure 4). However, one anomalous older age from GR indicates this reef may have reached sea level by 3,482 cal yBP, consistent with SR. Given no ages were reported from GR between 3,482 and 1,915 cal yBP, it is uncertain whether coral growth was persistent at GR and nearby lagoonal reticulate reefs during this 1,500-year period. Sustained reef growth during the hiatus period (2,905–1,915 cal yBP) is possible, considering published data that show *Porites* spp. microatolls aged 2,000–3,000 yBP within a ~3 km boundary of GR (McGregor et al., 2011), likely at comparable elevations. With samples reported in this manuscript only collected from the upper reef flat, it is likely the termination age of SR and GR were captured, but the full age range of these reefs may be undersampled. To capture the full age range, and to characterize past reef accretionary histories, coring through the reef surface is required. However, microatoll age data from Woodroffe et al. (2012) support the possibility of a hiatus in reticulate reef growth at the central, interior section of Kiritimati Island, where no ages between ~2,200 and 2,800 yBP were reported. Similar reef hiatus episodes have been reported in

Australia (Leonard et al., 2020; Perry & Smithers, 2011), Japan (Hamanaka et al., 2012) and Pacific Panama (Toth et al., 2012) and are often attributed to regional environmental or climatic changes. Woodroffe et al. (2012) show that coral growth persisted between 2,200 and 2,800 yBP at other locations on Kiritimati Island (the modern reef flat at Northeast Point and the interior reticulate fossil reefs near Southeast Point). This suggests that a possible hiatus in reef growth at Kiritimati was driven by localized changes in environmental conditions, rather than regional environmental or climatic drivers. Further coral age data from GR, SR, and surrounding reticulate fossil reefs would shed more light on this possible hiatus at Kiritimati Island. Overall, however, the variable coral composition and discrete age chronologies between SR and GR that we observe suggest that shifts in biophysical and hydrodynamic conditions occurred over the past 4,000 years (Figure 4). We invoke sea-level variability, storm ridge deposition and subsequent changes to biophysical conditions (e.g., flushing) inside the lagoon as potential driving factors for lagoon reef shutdown in a staged manner.

The presence of large microatolls (up to 4 m in diameter) at comparable elevations at both GR and SR indicate that reef growth at both sites occurred under similar and prolonged sea-level constraints (Figure S6). Early work at Kiritimati Island suggests that late Holocene sea-level fall during the period 1,500 yBP to present, following a mid-Holocene highstand, resulted in the emergence of the reticulate lagoonal reefs (Valencia, 1977; Woodroffe & McLean, 1998). However, recent reevaluations by the same authors contest this view and provide no evidence of a highstand (Woodroffe et al., 2012). Our results are inconclusive regarding the presence or nature of a mid-Holocene highstand. We show that atoll interior fossil reef surfaces at GR and SR, which include microatolls, are at comparable elevations. Both GR and SR are located between 0.5 and 2.0 m above sea-level datum (Figure S6), suggesting that sea-level persisted at a similar elevation between ~4,000 and 2,000 yBP when GR and SR flourished. The nature of sea-level change throughout the following 2,000 years to present remains unclear from our data set because of the absence of dated material collected within this age range. The similarity of fossil reef elevations implies that factors other than sea-level change and associated reef emergence must have contributed to the episodic shutdown of the reticulate reef flats, which occurred in a staged manner. Present day emergence of the fossil reefs in the interior of Kiritimati Island may result from a lowering of lagoon water levels when the reticulate lagoonal reefs were shut off from the open ocean. Higher lagoonal water levels compared to the open ocean have been observed in the modern lagoon of Kiritimati atoll, associated with tidal attenuation in the lagoon (Woodroffe et al., 2012) and in other modern atoll lagoon environments globally, associated with wave setup-driven water level gradients (Callaghan et al., 2006).

Deposition of storm-deposited rubble ridges at the atoll rim may have closed down ocean flushing to the previously open (now enclosed) reticulate lagoon network episodically during the late Holocene (Figure S5). Grothe et al. (2016) sampled and dated the extensive storm ridges, which extend up to 200 m inland, around the rim of Kiritimati Island, with samples dated between 6,000 yBP and modern. Most samples from locations nearest to GR and SR dated around or younger than 2,000 yBP (Grothe et al., 2016), indicating deposition in the late Holocene and a recent period of high storm activity. It is possible that these ridges enclosed reticulate lagoonal reefs and disconnected them from the open ocean. The resulting lack of wave forced flushing would have removed the wave setup gradient across the lagoon and consequently caused water level to fall. Modern analogs of extensive postcyclone coral rubble ridges, such as that deposited by Cyclone Bebe on reef flats in Tuvalu, can be extensive (Baines & McLean, 1976), and would effectively block cross-reef wave-driven water flow. In addition, the formation of islands on atoll rim reef flats can have the same impact as storm deposits in influencing lagoon flushing (Kench, 1998). Consequently, it is likely that storm deposits on the atoll rim had a marked impact on water level and environmental conditions in the reticulate lagoon network through the late Holocene, and forced emergence of both GR and SR. Due to the more interior location of SR than GR (GR is located closer to the atoll rim), it is likely that SR was enclosed and isolated from the open ocean earlier than GR. In addition to the greater storm ridge development, the timing of lagoon reef shutdown at SR (~2,905 cal yBP) and GR (~1,705 cal yBP) is also consistent with elevated tropical cyclone activity in the central Pacific 2,900–500 yBP (Bramante et al., 2020; Toomey et al., 2013). Storm ridge deposition would change biophysical conditions inside the lagoon as open ocean water exchange was cut off, and likely render the interior lagoonal reticulate system of Kiritimati Island devoid of modern coral growth. This would occur first by forcing shifts in community composition on the lagoonal reefs, before the lagoon became totally uninhabitable for corals due to further declines in water

quality. Lagoonal water quality conditions were likely very distinct from open ocean conditions (and prior well-flushed lagoon environments). Devoid of ocean flushing, and under arid tropical conditions, enclosed lagoons will rapidly transition to a brackish or hypersaline state (Saenger et al., 2006; Schmitt et al., 2019; Valencia, 1977) that would have been, and remain, unable to support coral communities.

Coral species zonation on reefs is well-demonstrated to reflect differing environmental conditions (Done, 1982). Marked differences in coral composition between SR (*Acropora*-dominated) and GR (*Porites*-dominated) suggest the sites developed under different hydrodynamic and biophysical conditions (e.g., temperature, salinity, turbidity). The abundance of branching *Acropora* spp. at SR indicates the site was a sheltered lagoonal reef, as fast-growing acroporids typically inhabit calm and high-light settings (Perry & Morgan, 2017; Roff et al., 2012). Similar coral communities are found in the modern open lagoon of Kiritimati Island, where lagoon-open ocean water exchange remains high. The dominance of *Acropora* spp., together with its older age, suggest that SR established whilst the lagoon was well-connected to the open ocean under clear and well-flushed conditions. The abundance of *in situ Tridacna* spp. across SR also supports this, as these mollusks are also found in shallow, high-light settings on modern reefs (Othman et al., 2010). In contrast, the preserved reef at GR likely developed later in the geomorphic evolution of the reticulate lagoon system, potentially either as biophysical conditions deteriorated as the lagoon began to shut down episodically, or under high wave energy conditions when this section of the lagoon was still connected to the open ocean. Coral communities at GR, which are dominated by stress-tolerant taxa (*Porites* spp. and *Fungia* spp.), are comparable to modern reefs inhabiting marginal lagoonal environments (Camp et al., 2019) as well as those that are exposed to high wave energy such as at Cecile Peninsula (that we report here in the supporting information), where coral communities are dominated by massive *Porites* spp. and spheroidal rhodoliths are abundant (Table S5 and Figure S4). The latter scenario is more likely, given the proximity of GR to the atoll rim and the abundance of rhodoliths at GR (Figure S5), which would suggest higher open ocean wave exposure than SR (where rhodoliths were not recorded) (Bosellini & Ginsburg, 1971; Perry, 2005).

In summary, our topographic, ecological, and age data from GR and SR at Kiritimati Island reveal that these two lagoonal reticulate reefs developed during temporally discrete episodes in the late Holocene and were comprised of significantly different coral communities (*Acropora*-dominated or *Porites*-dominated), indicating exposure to different environmental conditions. This dataset provides new insights into how large-scale changes to atoll morphology associated with storms can influence and control lagoonal water properties and thus lagoonal reef ecology and state. We conclude that the hydrodynamic shutdown of reticulate lagoonal reefs was most likely due to storm-deposited gravels at the atoll rim in the late Holocene, reducing open ocean flushing in parts of the atoll lagoon. This would have resulted in altered lagoonal biophysical conditions and lowered lagoonal water levels due to a lack of wave setup-induced water level gradients and wave flushing. Indeed, the eco-geomorphic roles of storms in atoll environments will become increasingly important to understand, given predicted increases in storm magnitude and frequency associated with climate change (Knutson et al., 2010). Larger and more frequently deposited storm ridges may have the potential to alter lagoon functioning, and impact the ecosystem services provided by these lagoon systems.

Data Availability Statement

Data that support the manuscript can be accessed through the general repository Fig Share: <https://doi.org/10.17608/k6.auckland.c.5324399.v1>.

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