Reefal microbial crusts found in Middle Holocene reef from Okinawa Island, the Ryukyu Archipelago

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Communicated by Hiroya Yamano (Editorial board member)

Abstract Reefal microbial crusts (RMCs) are fine-grained, non-skeletal carbonate crusts coating coralgal reef frameworks, and are locally common in late Quaternary reef deposits. They are interpreted as microbial carbonates produced by the growth and metabolism of benthic bacterial communities. Key questions remain concerning their uneven spatio-temporal distributions, formation process and controlling factors; the crusts have not yet been reported in the Ryukyu Archipelago. Here we report the first occurrence of brownish, few-centimeter-thick, fine-grained, non-skeletal crusts in a Middle Holocene reef core recovered at Naha New Port Pier, off the western coast of Okinawa Island, the Ryukyu Archipelago. The outer morphology of the crusts is either knobby or flat. The meso-scale fabric of the crusts is generally clotted and structureless, while a few crusts are weakly laminated or digitate. The slab core shows a biological succession from a bioeroded coral oriented upward, overlain by thin crusts of coralline algae and encrusting foraminifers, ending in a brownish, fine-grained, non-skeletal crust. Surface elemental mapping shows that the crusts are composed mainly of Ca and Mg (i.e., Mg-containing carbonate). X-ray diffraction analysis indicates that the crusts are composed predominantly of high-magnesium calcite, subordinate with aragonite and quartz. Petrographic observations show that the crusts are made mainly of peloidal micrite with irregular voids (cavities), associated with silt-sized bioclastic and siliciclastic grains. The crusts develop within a particular core depth and age range (4.6–6.1 m depth; ca. 7 ka), from which the crusts change downward and upward into encrusting bryozoan and foraminiferal crusts filled with micrite. Based on our observations, compared with previous studies, we conclude that brownish, non-skeletal carbonate crusts found in this study are RMCs, similar to those found in the last glacial, last deglacial and Holocene reef deposits from...
other coral reef regions (e.g., Tahiti and Great Barrier Reef). The RMCs likely developed in a low light/darker, semi-enclosed environment within primary cavities of high-energy, shallow-water coralgal frameworks. Since the study area is located adjacent to a river mouth and directly exposed to terrigenous sediment input from river runoff, multiple, local and global environmental factors associated with Holocene transgression and reef formation likely influenced the development of RMCs in the study area.

**Keywords** microbialite, northwest Pacific, Holocene transgression, peloid

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**Introduction**

The term “microbialite” was defined as “organo-sedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding detrital sediment and/or forming the locus of mineral precipitation” (Burne and Moore 1987). The benthic microbial community is composed dominantly of bacteria including cyanobacteria, associated with non-skeletal microalgae (Dupraz et al. 2011; Riding 2011a). Precipitated minerals are mainly carbonates and produced by the interaction of microbial growth and metabolism, cell surface properties, and extracellular polymeric substances (EPS) (Dupraz et al. 2011; Riding 2011a). Microbialite is classified into four different types based on meso-scale fabric, which refers to structures visible with the naked eye: stromatolite (laminated type), thrombolite (clotted type), dendrolite (dendritic type), and leiolite (structureless type) (Dupraz et al. 2011; Riding 2011a). Microbialites are known from the Archean and were common in the Proterozoic. Thereafter, microbialite abundance declined in surface environments after the Middle Ordovician and further after the Jurassic, likely due to reduction in carbonate saturation state and competition with unicellular eukaryotes and metazoans (Webb 1996; Riding 2011a; Wood 2011).

Neverthless, microbialites are still common in cryptic environments as well as in marine, hypersaline, freshwater, and even continental environments where precipitation is inorganically favored as well as where competitors are environmentally excluded (Webb 1996; Dupraz et al. 2011; Riding 2011a).

Reefal microbial crusts (RMCs) are crusts of microbialites found in reef environments, which are characterized by fine-grained, non-skeletal carbonates (Riding 2011b). The crusts have been previously recognized as submarine micritic cements (submarine lithification; Macintyre and Marshall 1988; Macintyre 2011), but now are widely interpreted as microbial carbonates (Riding 2011b). RMCs are as much as 20 cm thick, and locally constitute 80% of the reef structure (e.g., Camoin et al. 1999). RMCs represent the last stage of encrustation of coralgal frameworks during reef development, and play an important role in strengthening reef frameworks (e.g., Montaggioni and Camoin 1993; Webb 1996; Camoin et al. 1999; Seard et al. 2011). RMCs have been found in reef cores, outcrops and caves from Tahiti (Montaggioni and Camoin 1993; Camoin and Montaggioni 1994; Camoin et al. 1999; Camoin et al. 2006), the Great Barrier Reef (GBR) (Reitner 1993; Webb and Jell 1997; Webb et al. 1998; Jell and Webb 2012), Vanuatu, the Solomon Islands (Cabiocb et al. 1999; Cabiocb et al. 2006), Maldives (Gischler et al. 2008), St. Crox, the Caribbean Sea (Zankl 1993), and other coral-reef regions (reviewed in Riding et al. 2014). RMCs are also volumetrically important components of last glacial to last deglacial reef successions drilled during the Integrated Ocean Drilling Program (IODP) Expeditions 310 at Tahiti (Westphal et al. 2010; Seard et al. 2011) and 325 at the GBR (Webster et al. 2018; Braga et al. 2019). RMCs are more common in last glacial, last deglacial than in Holocene reefs (Riding 2011b; Riding et al. 2014). RMCs are generally composed of silt-sized peloids that trapped allochthonous bioclastic and siliciclastic grains (e.g., Camoin et al. 1999; Riding 2011b; Seard et al. 2011). In Tahiti and other regions, RMCs developed either simultaneously with coralgal communities (Westphal et al. 2010; Braga et al. 2019) or 100–500 years after coralgal communities (Gischler et al. 2008; Seard et al. 2011; Jell and Webb 2012).

However, key questions still remain unanswered regarding factors that control their formation and spatiotemporal distribution. Both biotic and abiotic (environmental) factors have been proposed to explain distribution of RMCs. Biotic factors include the volume and shape of
primary cavities in initial reef frameworks (Seard et al. 2011) and interspecific competition for space with metazoans and invertebrate encrusters (Riding 2011b). Abiotic factors include the last deglacial sea-level rise and subsequent Holocene stabilization (Cabioch et al. 2006; Gischler et al. 2008), decreasing light levels and wave energy (Zankl 1993; Camoin et al. 1999), increased nutrient availability and alkalinity from river runoff, groundwater seepage, upwelling, and the decomposition of organic matters (Camoin and Montaggioni 1994; Camoin et al. 1999; Cabioch et al. 2006; Westphal et al. 2010; Braga et al. 2019), changing alkalinity and pH in response to atmospheric pCO$_2$ (i.e., ocean acidification) (Riding et al. 2014; Braga et al. 2019), tectonic uplift rate (Cabioch et al. 2006), and water circulation (pumping of tidal flows and seawater flushing) (Cabioch et al. 2006; Gischler et al. 2008; Riding et al. 2014). Understanding the formation setting, formation age, and physical and chemical paleoenvironments such as water quality and seawater chemistry are crucial to solve the controlling factors for RMC development.

RMCs previously have not been reported from the Ryukyu Archipelago (Ryukyus). Previous researchers may have noted similar non-skeletal carbonate crusts, but have called them either “consolidated laminated mud” (e.g., Webster et al. 1998) or submarine micritic cements. Here we report the first RMCs found in a Middle Holocene reef core from Okinawa Island, the Ryukyus, where reef is basically shore attached (fringing type). In this paper, our scientific objectives are to (1) describe the stratigraphic occurrence of RMCs, (2) describe their petrographic and geochemical features, and (3) discuss their formation setting, controlling factors and spatio-temporal distributions in the Ryukyus. Our results indicate multiple, local and global environmental factors associated with Holocene transgression and reef formation likely constrained the development of RMCs in the study area. Our study also provides a rare example where significant RMCs developed adjacent to the mouth of a river, being directly exposed to terrigenous sediment input by river runoff.

Materials and methods

The studied cores were obtained on the Naha New Port Pier, where an offshore patch reef has been reclaimed (26°14’59.4"N, 127°40’15.1”E; Fig. 1). The drill site is

Fig. 1 Study area. A, Ryukyu Archipelago; B, Okinawa Island; C, Naha New Port Pier; D, location of drill site (yellow star) in the pier on a reclaimed patch reef.
located about 1.6 km off the mouth of a river (Fig. 1C). The elevation of the drill site is about 3 m above mean sea level. At the drill site, cores with an outer diameter of 66 mm (inner core diameter of about 46 mm) were recovered down to 8 m depth in August, 2013 using a rotary engine coring system without water supply. Since this drilling system enables recovery of unconsolidated sediments as well, the overall recovery was 87% and the remaining percentage is interpreted as primary cavities and some degree of compaction (Fig. S1).

Digital core images were taken using a core image scanner. Cores were described visually, with respect to sediment constituents and biotic composition. Corals were identified to the genus level; their growth form and direction, and the degree of macrobioerosion were noted. Growth direction of more than several-cm-thick coral colonies were determined based on the orientation of corallite walls. Crusts coating corals were described and classified into those formed by coralline algae (“algal crust”), possibly by benthic microbial communities (“microbial crust”), and by encrusting metazoans (including bryozoans) and foraminifers (“encrusting organisms”). Core sections where a coral was encrusted with crusts were selected and cut into slabs. A total of 25 core slabs with 1 cm in thickness were prepared from 3.0–6.9 m depth (Table 1). Long core sections were cut into smaller parts (e.g. samples NH4-09, -13). Each slab was scanned digitally to observe the type and degree of encrustation in detail.

Surface element mapping of the slabs was performed using X-ray analytical microscopy (HORIBA XGT-7200). Prior to the measurements, each slab was embedded in epoxy resin to avoid fragmentation, polished, ultrasonically cleaned, and dried. The slab surface was analyzed using energy dispersive X-ray fluorescence with an X-ray beam diameter of 100 μm. Beam current was 1.0 mA with a voltage of 30 kV. Elements analyzed were Ca, Mg, Sr, Si, Al, P, S, K, Mn, and Fe. Analytical area was ~100 mm². Analytical time was 360 s (6 min). Elemental mapping was expressed as 8 bit (256 levels) grayscale with white as high intensity and black as low intensity.

Petrographic thin sections were prepared from selected slabs, and observed using transmitted light under an optical microscope with crossed nicols. Observations in-

### Table 1: Core depth, biotic composition, and meso-scale fabric of reefal microbial crusts of slab samples from core NH4. P, present.

| Sample (NH4-) | Top depth (cm) | Bottom depth (cm) | Algal crust | Bioerosion | Encrusters | IBFM | SM | LM | DM | MCD |
|---------------|----------------|-------------------|-------------|------------|------------|------|----|----|----|-----|
| 1             | 300            | 305               | P           | P          | P          | P    |     |    |    |     |
| 2             | 310            | 315               | P           | P          | P          | P    |     |    |    |     |
| 3             | 371            | 376               | P           | P          | P          | P    |     |    |    |     |
| 4             | 387            | 394               | P           | P          | P          | P    |     |    |    |     |
| 5             | 394            | 400               | P           | P          | P          | P    |     |    |    |     |
| 6             | 410            | 420               | P           | P          | P          | P    |     |    |    |     |
| 7             | 437            | 442               | P           | P          | P          | P    |     |    |    |     |
| 8             | 451.5          | 459               | P           | P          | P          | P    |     |    |    |     |
| 09-top        | 459            | 476               | P           | P          | P          | P    |     |    |    |     |
| 09-middle     | 459            | 476               | P           | P          | P          | P    |     |    |    |     |
| 09-bottom     | 459            | 476               | P           | P          | P          | P    |     |    |    |     |
| 10            | 483.5          | 489               | P           | P          | P          | P    |     |    |    |     |
| 11            | 489            | 500               | P           | P          | P          | P    |     |    |    |     |
| 12            | 500            | 504               | P           | P          | P          | P    |     |    |    |     |
| 13-top        | 504            | 515               | P           | P          | P          | P    |     |    |    |     |
| 13-bottom     | 504            | 515               | P           | P          | P          | P    |     |    |    |     |
| 14            | 523.5          | 527               | P           | P          | P          | P    |     |    |    |     |
| 15            | 527            | 534               | P           | P          | P          | P    |     |    |    |     |
| 16            | 542            | 545               | P           | P          | P          | P    |     |    |    |     |
| 17            | 554            | 559               | P           | P          | P          | P    |     |    |    |     |
| 18            | 566            | 571               | P           | P          | P          | P    |     |    |    |     |
| 19            | 575.5          | 583               | P           | P          | P          | P    |     |    |    |     |
| 20            | 607            | 613               | P           | P          | P          | P    |     |    |    |     |
| 21            | 623            | 628.5             | P           | P          | P          | P    |     |    |    |     |
| 22            | 633            | 638               | P           | P          | P          | P    |     |    |    |     |
| 23            | 640            | 648               | P           | P          | P          | P    |     |    |    |     |
| 24            | 669            | 673               | P           | P          | P          | P    |     |    |    |     |
| 25            | 683            | 689               | P           | P          | P          | P    |     |    |    |     |

IBFM: intraskeletal and boring-filling microbialite. SM: structureless microbialite. LM: laminated microbialite. DM: digitated (knobby) microbialite. MCD: microbialite coated debris.
clude distribution, size, shape and abundance of minerals, grains and cavities.

Some parts of brownish non-skeletal crusts (NH4-13, 16, 17, 23) were cut, ultrasonically cleaned using Milli-Q water, dried, and pulverized for X-ray diffraction (XRD) analysis. The powdered samples were analyzed using an X-ray diffractometer (RIGAKU RINT Ultima+; CuKα radiation, 40 kV voltages; a 30 mA intensity and 2°/min (2θ) speed) to quantify the mineral composition of aragonite (26.6°2θ), low-Mg calcite (LMC: 29.4°2θ), high-Mg calcite (HMC: around 29.8°2θ) and quartz (26.2°2θ) by measuring their peak heights (Milliman 1974). The analyses were run from 3 to 90°2θ. MgCO₃ contents of HMC (mol%) were estimated based on empirical curves between d₁₀⁴ values and MgCO₃ composition in carbonate crystals (Zhang et al. 2010).

Five corals oriented upward with different depth intervals were selected for radiocarbon (¹⁴C) dating. ¹⁴C ages of the selected corals were measured using accelerated mass spectrometry (AMS) at Beta Analytics, Inc. Prior to the ¹⁴C measurement, we confirmed whether original coral mineralogy was retained or not with XRD analysis. Then, we cleaned coral samples with Milli-Q water and performed a chemical pre-treatment with HCl to avoid surface contamination. All conventional ¹⁴C ages were calibrated using the Marine13 dataset (Reimer et al. 2013), a ΔR (regional difference from the average global marine reservoir age) value of 10±37 years (Araoka et al. 2010), and the calibration software OxCal v4.2.4 (Ramsey 2009). Vertical accumulation rates of coralgal frameworks were calculated from the depth interval of dated corals oriented upward.

**Results**

**Lithology and biotic succession**

Except for reclaimed deposits in the upper part of the core (0–2.8 m depth), the drilled core succession from 2.8 to 7.9 m depth is composed of coral skeletal framework partly filled with unconsolidated bioclastic sediment (coral rubble, skeletal gravel and sand, lime mud; Fig. 2). ¹⁴C ages of coral colonies oriented upward indicate that the drill core is Middle Holocene (younger than 7540 mean cal BP), and mostly developed between 7500 and 6700 mean cal BP (Fig. 2, Table 2). Accumulation rates of coralgal frameworks range from 2.7 to 5.7 mm yr⁻¹. The highest rate is found from 6.5 to 4.4 m depth.

Corals oriented upward are more common in the lower part of the core (4.7–7.6 m depth), while corals oriented downward are more common in the upper part of the core (3.0–4.7 m depth; Fig. 2). Dominant corals and their growth forms differ by core depth. A 70 cm-thick massive
Goniastrea colony is found at 6.9–7.6 m depth. Tabular Isopora colonies are found at 6.3–6.6 m depth. Tabular Acropora colonies are common at 3.7–6.3 m depth. Most corals oriented upward are heavily bioeroded by boring organisms (e.g., bivalves, sponges). Bored cavities, as much as 1 cm across, are common near the surface of coral colonies (Fig. 3).

Surfaces of coral colonies oriented upward are encrusted with thin crusts (several mm thick) of crustose coralline algae (CCA; Fig. 3, Table 3). Common coralline algae include Porolithon gr. onkodes, Lithophyllum gr. prototypum, and Harveyolithon gr. munitum. Peyssonneliacean algae occur associated. The thin crusts of CCA are overlain by encrusting metazoans (bryozoan, vermetid gastropods) and foraminifers (Carpenteria sp., Homotrema rubrum, Acervulina sp.), and/or non-skeletal, fine-grained crusts (Figs. 3, S2). Encrusting metazoans and foraminiferal crusts are common toward the upper and lower parts of the core (3.0–5.3 and 6.3–6.9 m depth), while brownish, fine-grained, non-skeletal crusts are found at a limited depth of the core (4.6–6.1 m depth; Fig. 2).

Fine-grained, non-skeletal crusts

Brownish, fine-grained, non-skeletal crusts coat coralgal frameworks as well as partially fill the small cavities in bored coral skeleton (Fig. 3C–G). The thickest crust is ~1.8 cm thick at around 5.5 m depth (Fig. 3F). The outer morphology of the crusts is either knobby (club shaped/digitate; NH4-16, 17; Fig. 3F, G) or flat (NH4-13-top; Fig. 3E). Knobby and flat morphologies are clearly observed at relatively thick crusts. Their growth direction is generally upward (NH4-13-top, -16; Fig. 3E, F), but some crusts grew laterally (NH4-17; Fig. 3G). The meso-scale fabric of the crusts is generally clotted and structureless (i.e., having no distinct internal texture; NH4-16; Fig. 3F), while some are weakly laminated (NH4-13-top; Fig. 3E) or digitate (NH4-17; Fig. 3G).

Element mapping shows that Ca is the most intense element throughout sections examined (Figs. 4 and S3). Brownish non-skeletal crusts coating coral skeleton is composed of Ca, associated with Mg, suggesting Mg-containing carbonate materials. Intensity contrasts between coral skeleton and crusts; Al and Mg are more common in crusts than coral skeleton, while Sr is more common in coral skeleton than crusts. Other elements considered (P, S, K) are scattered throughout the sections examined. Si and Fe are scattered patchy in crusts, suggesting the presence of silicate and iron-oxide minerals.

X-ray diffraction results (Table 4) show that three of four crusts examined are mainly composed of HMC (~80%), subordinate with aragonite (5–8%) and quartz (~9%). Only one sample (NH4-23) contains LMC (9.6%) and has a different mineral composition (HMC: 51%, aragonite: 26%, quartz: ~13%). MgCO$_3$ contents of HMC are 12–15 mol%.

Petrographic observations show that brownish, non-skeletal carbonate crusts are composed of dense clotted to peloidal micrites mixed with bioclasts and siliciclastic grains (Fig. 5A, B). The micro-scale fabric is generally structureless, but irregular voids (cavities) of various shape and size are observed (Fig. 5A–D), and several cavities are rarely and weakly aligned (Figs. 5A, S5B). The peloids reach 50 μm in diameter (Fig. 5C, D). Bioclasts are mainly silt-sized coral and mollusk shell fragments (Fig. 5B, C). The siliciclastic grains including silt-sized quartz and feldspar are minor in abundance (Fig. 5B, C). Bored spaces in coral skeleton are partially or entirely filled with peloidal aggregates with few silt-sized bioclastic and siliciclastic grains (Fig. S5E, F). Encrusting
Fig. 3  Core slabs showing the distribution and morphology of reefal microbial crusts and encrusting metazoan and foraminiferal crusts. a, coralline algae; b, bryozoan; c, coral; e, encrusting organisms; m, reefal microbial crust. A, NH4-01; B, NH4-04; C, NH4-08; D, NH4-09-top; E, NH4-13; F, NH4-16; G, NH4-17; H, NH4-23. Arrows indicate bored cavities. Rectangular frames indicate the locations of elemental mapping shown in Figs. 4 and S3. Scale bar = 1 cm.
bryozoans and foraminifers are more common both upward and downward from core depth interval where non-skeletal carbonate crusts are common (Fig. S4A, C, S5G), but dense micrites still fill inter- and intra-granular spaces of encrusting organisms and bioclasts (Fig. S4B, D, S5H). This biotic composition change is reflected by the XRD results above (NH4-23; Table 4). Grain sizes of associated bioclasts and siliciclastic grains are larger in the encrusting organisms (Fig. S4B, S5H) than those found in the non-skeletal carbonate crusts.

### Discussion

#### Comparison with other reefal microbial crusts

Brownish, fine-grained, non-skeletal, high-magnesium calcite crusts found in the studied reef core are similar to RMCs reported in other reefs (e.g., Camoin et al. 1999; 2001; Richardson et al. 2004; Trincardi et al. 2006).

| Sample (NH4-) | Dawsonithion convicium | Harveyithion gr. munitum | Hydroolithon reinboldii | “Hydroolithon” brevilocauda | Lithoporella melobesoides | Lithophyllum insipidum | Lithophyllum gr. kotschyanum | Lithophyllum gr. prototypum | Mastophora pacifica | Melvynnea erubescens | Mesophyllum mesomorumphum | Poroithon gr. onkodes | Harveyithion or Hydroolithon sp. | Mastophora or Lithoporella sp. | Peyssonneliaceae algae |
|---------------|------------------------|--------------------------|------------------------|---------------------------|------------------------|------------------------|--------------------------|------------------------|-------------------------|----------------------|------------------------|------------------------|------------------------|------------------------|------------------------|
| 01            | P                      |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 02            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 03            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 04            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 05            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 06            | P                      |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 07            | ?                      |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 08            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 09-top        |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 09-middle     |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 09-bottom     |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 10            | P                      |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 12            | P                      |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 13-top        | P                      |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 13-bottom     | P                      |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 14            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 15            | ?                      |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 16            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 17            | P                      |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 18            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 19            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 20            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 21            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 22            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 23            |                        |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 24            | P                      |                          |                        |                           |                        |                        |                          |                        |                         |                      |                       |                        |                        |                        |                        |
| 25            | P                      | P                        | P                      |                           |                        |                        | P                        |                        |                         |                      |                       |                        |                        |                        |                        |

*Table 3* List of coralline algae identified in thin sections from core NH4. P, present; ?, possibly present.
Fig. 4 Microprobe mapping of major elements (Ca, Mg, Sr, Si, Al, P, S, K, Mn, and Fe) using X-ray analytical microscopy. A, NH4-9-top; B, NH4-13-top; C, NH4-16; D, NH4-17. For the locations measured, see Fig. 3.
The outer morphology of the crusts is either knobby (club shaped/digitate) or flat, which is the typical macro-scale fabric of RMCs (Camoin and Montaggioni 1994; Riding 2011b) and microbialites in general (Dupraz et al. 2011; Riding 2011a).

The meso-scale fabric of the non-skeletal carbonate crusts in this study is clotted and structureless, but a few are weakly laminated or digitate. The structureless mesofabric refers to “leiolite” (Riding 2000) or “structureless microbialite” which have been found in the last glacial
and deglacial succession beneath the shelf edge of the GBR (Braga et al. 2019). Weakly laminated or digitate mesofabrics are similar to laminated and digitate microbialites reported from other regions, respectively (Zankl 1993; Camoin et al. 1999; Cabioch et al. 2006; Gischler et al. 2008; Seard et al. 2011; Jell and Webb 2012; Braga et al. 2019). Small cavities in bored coral skeleton are partially filled by peloidal aggregates, corresponding to “intraskeletal and boring-filling microbialite (IBFM)” also found in the last deglacial succession from the GBR (Braga et al. 2019). IBFM likely develops in skeletal voids and borings either coevally (Westphal et al. 2010; Braga et al. 2019) or soon after death of corals (Seard et al. 2011).

The carbonate crusts are generally <1 cm thick, and thinner than RMCs reported from the other regions (up to 20 cm thick) (Camoin et al. 1999; Cabioch et al. 2006; Gischler et al. 2008; Seard et al. 2011; Braga et al. 2019). Since thicker and thinner RMCs are generally found in last deglacial and Holocene reef successions, respectively (Riding et al. 2014), thickness is partly attributed to formation age. The thin crusts are dominated by structureless mesofabric in the studied core. Structureless microbialites are generally the first microbialite mesofabric coating over coralgal frameworks, followed by laminated and digitate fabrics in the GBR (Braga et al. 2019).

The micro-scale fabrics of the carbonate crusts are composed of dense, clotted to peloidal micrites, with cavities and subordinate silt-sized bioclastic and siliciclastic grains. These microfabric features are similar to those of RMCs reported from other reef regions (Montaggioni and Camoin 1993; Camoin and Montaggioni 1994; Camoin et al. 1999; Cabioch et al. 2006; Gischler et al. 2008; Westphal et al. 2010; Seard et al. 2011; Braga et al. 2019) and correspond to “mixed micritic-agglutinated microfabric” (Dupraz et al. 2011). Lipid biomarker data and stable sulfur isotope results confirmed that sulfate-reducing bacteria played an intrinsic role in the precipitation of those carbonate crusts (Heindel et al. 2012; Braga et al. 2019). Bacterial degradation of extracellular polymeric substances (EPS) and coral mucus within microbial mats results in anoxic micro-environments, which might favor carbonate precipitation. Peloidal micritic masses are widely recognized as a product of the micro-biologically mediated precipitation of high-magnesium calcite within and around active clumps of coccoid bacteria (Chafetz 1986; Riding et al. 1991; Camoin and Montaggioni 1994; Riding 2000; Shiraishi et al. 2017). Silt-sized bioclasts and siliciclastic grains appear to be floating in and trapped by peloids, suggesting that surrounding peloids were formed within soft and sticky EPS during the time of grain deposition (Camoin and Montaggioni 1994).

Previous studies reported the presence of microbial filament remains (Camoin and Montaggioni 1994; Cabioch et al. 2006; Heindel et al. 2009a; Heindel et al. 2009b), geochemical features such as chemical composition (Camoin and Montaggioni 1994; Camoin et al. 1999; Webb and Kamber 2000; Cabioch et al. 2006), stable carbon and oxygen isotope ratios (Montaggioni and Camoin 1993; Reitner 1993; Camoin and Montaggioni 1994; Camoin et al. 1999; Cabioch et al. 2006; Braga et al. 2019), and biomarkers (Camoin et al. 1999; Heindel et al. 2012; Gischler et al. 2017; Braga et al. 2019) as confident evidence of the microbial origin of RMCs. Based on our observations in comparison with previous studies, we conclude that brownish, fine-grained, non-skeletal carbonate crusts found in this study are RMCs, similar to those found in last glacial, last deglacial and Holocene reef deposits from other coral reef regions.

Formation setting

RMCs in the Ryukyu Holocene reef developed on the surface and intraskeletal space of the reef frameworks (Fig. 6). The RMCs represents the last stage of encrustation of corals oriented upward, overlain by coralline algae and encrusting metazoans and foraminifers. These biotic successions are consistent with those in previous reports from Tahiti (Montaggioni and Camoin 1993; Camoin and Montaggiogni 1994; Camoin et al. 1999; Westphal et al. 2010; Seard et al. 2011), the GBR (Braga et al. 2019), Vanuatu (Cabioch et al. 2006), and Maldives (Gischler et al. 2008). As in other reef regions, corals are mostly tabular forms of Acropora spp. and Isopora sp., associated with the massive form of Goniastrea sp. (Fig. 2). This assemblage corresponds to the present-day, high-energy, very shallow water, reef-crest environment around the Ryukyus (Hongo 2012). The coral surfaces were heavily bioeroded by boring metazoans (e.g., sponge, bivalves;
Fig. 3) and microorganisms, indicating some periods of exposure of coral skeletal surfaces after death of corals. These bioeroded corals are over lain by thin crusts (several mm thick) of crustose coralline algae (CCA; Fig. 3), associated with encrusting foraminifers (e.g., *Acervulina* sp., *Carpenteria* sp., *Homotrema rubrum*; e.g., Fig. S5C). The CCA assemblage is similar to those reported from the Ryukyus (Iryu 1992) and other regions (e.g., Humblet et al. 2019). The taxonomic composition of thin crusts corresponds to that of Assemblage A in the Ryukyus (Iryu 1992) and assemblage aA2 in IODP Exp. 325 in cores from the GBR (Humblet et al. 2019), indicating a paleo-water depth of 0–20 m. These results suggest that coralgal reef frameworks developed continuously in a high-energy, shallow-water environment.

RMCs developed in a limited range of core depth and age in the studied core (4.6–6.1 m depth, corresponding to ca. 7300–7000 cal BP; Fig. 6). According to Kawana (2011), the relative sea level at ca. 7 ka was almost at the present sea level in Okinawa Island. Considering that the
elevation of the core top is +3 m higher than the present sea level, the core depth range above corresponds to 1.6–3.1 m below sea level at ca. 7 ka. Previous studies also reported that RMC abundance decreased sharply around 6000 years ago in Tahiti (Camoin et al. 1999; Seard et al. 2011) and Vanuatu (Cabiocch et al. 2006). In Maldives, they formed only between 8000 and 7500 cal BP (Gischler et al. 2008). The limited depth range of RMCs in this study is consistent with a core depth interval with relatively fast accumulation rates (>5 mm yr⁻¹; Table 2). Rapid reef framework development likely resulted in producing more primary cavities within coralgal frameworks, which are shown in the drill core as horizons with no recovery or unconsolidated sediment infills (Figs. 2, S1). The primary cavities provided cryptic (i.e, low light/darker, semi-enclosed) environments, which are not favorable for photophilic organisms to colonize, but are likely favorable for microbial communities.

Controlling factors

Both biotic and abiotic (environmental) factors have been proposed to explain spatio-temporal distribution of RMCs. Our observations are consistent with Seard et al. (2011) that reefal microbialites develop in frameworks dominated by branching, thin encrusting, tabular and robust branching coral colonies, which built more primary cavities in the reef frameworks. This is supported by the absence of RMCs in and around a massive Goniastrea colony at 6.9–7.6 m depth (Fig. 2). However, the limited core depth and age in RMC development is not only explained by the volume and shape of the primary cavities, but also was likely constrained by Middle Holocene transgression and reef formation in the Ryukyus (e.g., Takahashi et al. 1988; Yamano et al. 2001; Kan and Kawana 2006; Hongo and Kayanne 2009, 2010; Kan 2011; Kawana 2011). Following the Holocene transgression, relative sea level around Okinawa Island stabilized at ca. 6 ka, reached the highest at 1.9 m above the present sea level, and lowered thereafter (Kawana 2011). Considering that the relative sea level at ca. 7 ka was almost at the present sea level (Kawana 2011), the location of coastline was almost the same as the present line, except that the coasts were not surrounded by fringing reefs at that time (Mezaki 1985). Since the study area is located off the mouth of a river (Fig. 1), the study area was directly exposed to terrigenous sediment input by river runoff, likely resulting in turbid environments. As reef frameworks rapidly developed upward during the Holocene transgression, low light, semi-enclosed primary cavities were formed inside the frameworks. These cryptic environments were subjected to the accumulation of terrigenous sediment flux. This is supported by the presence of siliciclastic silt grains (quartz and feldspar; Fig. 5) as well as some elements characteristic of silicate and clay minerals (Al, Si, K, Mn and Fe; Fig. 4) in the RMCs. Such conditions likely induced increasing nutrient availability and alkalinity as well as decreasing light and energy conditions within the cryptic cavities.

Subsequent Middle to Late Holocene relative sea-level stabilization and fall and reef formation (Yamano et al. 2001; Kawana 2011) likely caused the decline of RMC development after 6 ka in this study area as well as worldwide. The relative sea-level stabilization and fall caused reef accretion not vertically but horizontally (seaward), resulting in the development of reef crest and back-reef lagoon in the Ryukyus (e.g., Yamano et al. 2001; Kan 2011). Such horizontal reef accretion likely resulted in less development of new cryptic cavities within reef frameworks because reef surface and primary cavities were exposed to more open, better illuminated and higher water energy conditions, and infilled by coral rubble and skeletal sediments derived from the reef crest by strong breaking waves. These are inferred by the dominance of coral colonies oriented downward and detrital facies (Fig. 2) as well as the dominance of sand-sized grains in the encrusting bryozoans and foraminiferal crusts (3.0–5.3 m depth; Figs. S4B). The development of reef crest and back-reef lagoon also shifted the accumulation of terrigenous sediment flux landward, resulting in decreasing nutrient availability and alkalinity as well as increasing light intensity in the marginal reef frameworks. Such environmental changes are likely more favorable for photophilic encrusting organisms than microbial communities. The decline of RMCs is also likely related to continuously decreasing seawater carbonate saturation state in response to increasing levels of atmospheric CO₂ during the last deglacial and Holocene periods (Riding et al. 2014; Braga et al. 2019). Therefore, multiple factors including both
local and global (climate changes) origins associated with Holocene transgression and reef formation are likely involved in the development and demise of RMCs in the study area.

Spatio-temporal distribution in the Ryukyus

RMCs may be ubiquitously found in Middle Holocene reef deposits from the Ryukyus. Since previous studies on Holocene reefs using drill cores and uplifted reef terraces focused on patterns of reef growth and development as well as coral assemblages in response to Holocene sea-level change and tectonic movements, cements and encrusting organisms have not been described in detail (e.g., Takahashi et al. 1988; Webster et al. 1998; Yamano et al. 2001; Kan and Kawana 2006; Hongo and Kayanne 2009, 2010; Kan 2011). However, Webster et al. (1998) noted mud facies that “is composed of consolidated laminated mud with associated coral rubble fragments and is limited to the middle sections of cores at core depths of 2–12 m” in Holocene drill cores from Kikai Island. The consolidated laminated mud likely corresponds to RMCs in this study. Similar carbonate crusts are also shown in slab core photographs of drill cores taken in the Sekisei Barrier Reef (Kan and Kawana 2006). A several millimeter-thick crust coats in situ tabular Acropora coral colonies or fills the space between in situ branching Acropora coral and coralline algae. 14C ages of these corals are ca. 7530 and 7140 cal BP (Kan and Kawana 2006), respectively, which are similar in age to those obtained in this study. These observations suggest that RMCs are common beneath modern reef surfaces in the Ryukyus and likely developed in a certain Middle Holocene time period. Given the importance of understanding how such crusts respond to reef development and changing seawater chemistry (e.g., ocean acidification), additional reef coring investigations are necessary to better constrain the age and environmental settings of the development of RMCs in this region.

Conclusions

Thin (<1 cm), brownish, fine-grained, non-skeletal, high-magnesium calcite crusts found in the Ryukyu Holocene reef core are reefal microbial crusts (RMCs), which are crusts of microbial carbonates, typically found in primary cavities of late Quaternary reef frameworks. RMCs developed on the surface and intraskeletal space of coralgal reef frameworks in limited core depth and age ranges (1.6–3.1 m below present sea level and ca. 7 ka) in a single core. Multiple factors of both local and global origin associated with Holocene transgression and reef formation are likely involved in the development of RMCs in the study area, where the reef developed adjacent to a river mouth and was directly exposed to terrigenous sediment input from river runoff. RMCs are likely common beneath modern reef surfaces in the Ryukyus and developed in a certain Middle Holocene time period. Given the importance of understanding how such crusts respond to reef development and changing seawater chemistry (e.g., ocean acidification), additional reef coring investigations are necessary to better constrain the age and environmental settings of the development of RMCs in this region.

Compliance

Permission for core drilling was obtained from Urasoe City.

Acknowledgement

We thank S. Minei and Y. Kawasaki for their helps in core analyses. We thank F. Shiraishi for his discussion on RMCs. We also thank Center for Advanced Marine Core Research, Kochi University for the permission to use the core scanner and other facilities, and Center for Research Advancement and Collaboration, University of the
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Ryukyus for the use of X-ray analytical microscope and X-ray diffractometry, respectively. This work was partly supported by JSPS KAKENHI Grant Numbers JP25242026, JP16H02940, JP16H06309. We thank H. Kayanne and G. E. Webb for their constructive comments on the manuscript.

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*ESM Figs. S1–S5 can be downloaded from the J-STAGE website:
https://doi.org/10.3755/galaxea.22.1_9

Received: 31 January 2020
Accepted: 4 July 2020

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