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Late Holocene reef ecosystem baseline: Field evidence from the raised reef terraces of Kodakara and Kikai Islands, Ryukyu Islands, Japan

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To better understand and evaluate how present-day and future reef ecosystems are being impacted by natural climate change and human activity, it is important to establish reef ecosystem baselines from paleoecological records. Here we present paleoecological data, including coral cover and genus and species composition, for two raised reef islands (Kodakara and Kikai islands) located in the Ryukyu Islands (Japan) covering the last 2.4 and 4.1 kyr, respectively. Evidence of a mean cover of 20–40% coral on pristine reefs at the study sites was found for a millennial-scale period of ocean environment stability, in terms of sea level, solar radiation, and sea surface temperature. This coral cover has been maintained on the modern reef at Kikai Island since at least 4.1 kyr ago. The coral community was a reef crest–upper reef slope community, with *Acropora* and *Goniastrea* as the dominant genera and *Acropora digitifera* and *Goniastrea retiformis* as the dominant species from the late Holocene to present. Millennial-scale persistence of *A. digitifera* and *G. retiformis* may have been influenced by a strong Kuroshio Current, increased genetic diversity, and an increased potential for adaptation to environmental conditions. Our coral cover and species composition results provide important information for the development of effective reef restoration plans in light of the likely future degradation of reefs.

1. Introduction

Coral reefs have been subject to recent dramatic declines as a consequence of both local and global impacts (e.g., Cramer et al., 2012). Local impacts include sediment input, coastal development, and overfishing (e.g., Bellwood et al., 2012; Burke et al., 2011), while global impacts are associated with the consequences of contemporary climate change, including elevated sea surface temperatures (SSTs) and ocean acidification (Gattuso et al., 2014). Additional impacts, such as outbreaks of disease (Carpenter et al., 2008) and recurring outbreaks of crown-of-thorns sea stars (*Acanthaster planci*) (De'ath et al., 2012), have caused a decrease in coral cover and a loss of coral species diversity on reefs worldwide. In this context, various reef restoration strategies including coral transplantation have been conducted on many reefs (Horoszowski-Fridman et al., 2011; Omori et al., 2016). However, the availability of pristine coral reef ecosystems largely free of anthropogenic influences for use in evaluating reef restoration procedures is extremely limited. To aid the development of effective reef plans for the restoration of degraded reefs in the future, information on pre-industrial era coral reefs and their responses to natural environmental change is essential. In particular, a change in coral species and its cover should be assigned priority over other species in terms of the reef restoration plan.

In assessing the potential of reefs to survive major disturbance, Pandolfi et al. (2006) surveyed nine uplifted early to mid-Holocene (11.0–3.7 ka, where 1 ka = 1000 years ago) reefs of the Huon Peninsula (Papua New Guinea). The most striking coral mortality

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events occurred 9.1–9.4 ka, influenced by the deposition of volcanic ash. Following the disturbance, resettlement of corals and subsequent reef growth were rapid (<100 years), but the coral community shifted from *Isopora palifera* in the arborescent *Acropora* group prior to disturbance to the *Acropora humilis* and *A. hyacinthus* groups post-disturbance. To understand disturbances caused by human activity, Roche et al. (2011) compared modern and mid-Holocene coral communities at King Reef, in the central Great Barrier Reef (Australia), where water quality has declined since European settlement. They found no marked shifts in community composition (e.g., *Acropora*, *Porites*, and *Turbinaria*) and diversity, suggesting the long-term persistence of a resilient coral assemblage over this time period. Additionally, a series of hiatus events occurred at 5.9–5.8 ka, 4.4–4.0 ka, and 3.3–3.2 ka at Kodakara Island in the Ryukyu Islands, Japan; these were caused by low SSTs, resulting from a weakened Kuroshio Current, and sea level oscillations (Hamanaka et al., 2012, 2015). The coral genera diversity has gradually decreased as increased in hiatus, which was particularly characterized by the dominance of *Acropora* (Hamanaka et al., 2012). Genera-specific responses to environmental change in the Indo-Pacific and Caribbean regions were also reported (e.g., Aronson and Precht, 1997; Aronson et al., 2005; Perry et al., 2008). However, it is unclear whether there was a change in coral species in response.

Records of coral cover provide important data for assessing conditions on current coral reefs (De'ath et al., 2012). According to the result of coral cover on 2258 reef surveys from 214 different reefs in the whole Great Barrier Reef, the coral cover decreased from 28.0% to 13.8% over the period 1985–2012, with the decline influenced by tropical cyclones, outbreaks of *A. planci*, and coral bleaching (De'ath et al., 2012). The relatively pristine northern region showed no overall decline in this period, as a consistent cover of approximately 24% was found (De'ath et al., 2012). Webster et al. (1998) reported coral cover at five sites, Shitooke, Nakazato, Kadon, Nakaguma, and Araki, on raised Holocene reef terraces at Kikai Island (Ryukyu Islands). At Kadon reef the coral cover varied according to genus; for example, the cover for *Acropora* spp. and the family Merulinidae varied by 10–60% and approximately 0–20%, respectively. The total coral cover decreased from 40% to 20% in response to decreasing SSTs over the period 3.8–3.4 ka, when SSTs reached an average annual minimum of approximately 18 °C, and declined further below this temperature (Abram et al., 2001); 18 °C is generally considered to be the critical minimum temperature for reef growth (Veron, 2011). *Acropora* spp. recovered rapidly at the end of the cool event, as a consequence of coral recruitment, but the Merulinidae component of the community did not recover (Abram et al., 2001). However, records of coral cover from past pristine reefs to present reefs are poorly documented.

Current global environmental factors, such as increasing SST, changes in sea level and ocean circulation, and local factors, such as sediment discharge, may cause changes in the future biogeographic patterns of corals. Previous studies showed that increasing SST threatened the stability of species composition on reefs worldwide (Loya et al., 2001; Grottoli et al., 2014). *Acropora* species (e.g., *Acropora digitifera*) are susceptible to thermal stress events in Ryukyu Islands (Loya et al., 2001). In contrast, thermal stress-tolerance *Dipsastraea* species (e.g., *Dipsastraea favus*) and *Porites* species (e.g., *Porites lutea*) survived on the reefs in the Ryukyu Islands (Loya et al., 2001). The global warming may cause poleward range shift and/or expansions in coral species distribution (Yamano et al., 2011). To effectively conduct reef restoration in the future, information on historical background of the species in response to environmental changes will be required.

Here we present quantitative ecological data on coral cover and genus/species composition for two raised reef islands, Kodakara and Kikai islands, at the Ryukyu Islands, in the northwest Pacific; the data covers the last 2.4 kyr for Kodakara Island and the last 4.1 kyr for Kikai Island. The goal of the present study is: (1) to obtain quantitative records of coral cover from the past to the present on the study reefs, based on a line intercept transect method, (2) to reconstruct genus- and species-level records of corals from the reefs, (3) to assess whether there were discernible differences in coral cover, and the cover of genera and species throughout the time period, in relation to changes in environmental factors, (4) to identify dominant corals and reconstruct their biogeography from the past to the present, by comparing the pattern of corals from the surrounding region, and (5) to project coral reefs on the study sites, in response to future environmental changes, for a basic information about effective reef plans for the restoration.

2. Regional setting

2.1. Ryukyu Islands

Ryukyu Islands (Fig. 1A) are located in the path of the Kuroshio Current, a warm western boundary current in the northwest Pacific Ocean. The islands comprise one of the regions having the greatest diversity of coral reef species worldwide (Veron, 2000). Coral reefs in the region have recently been degraded during intervals of high SST (Loya et al., 2001; van Woesik et al., 2011). Short-term high turbidity levels in nearshore waters of the islands, resulting from anthropogenic runoff, have reduced the resilience of *Acropora* species (Hongo and Yamano, 2013). Coral cover has deceased as a consequence of multiple disturbances, including increased SST, physical damage caused by typhoons, and most likely sediment input from Ishigaki Island (Harii et al., 2014). A change in coral taxa has been observed, characterized by a shift in the dominant corals from branching *Montipora* and *Acropora* to *Heliopora coerulea* and massive and branching *Porites* (Harii et al., 2014).

2.2. Kodakara Island

Kodakara Island (29° 13.4′ N, 129° 19.5′ E; Fig. 1B) is located in the northern Ryukyu Islands, and is on the main path of the Kuroshio Current. There are no major rivers on the Island. The coral reefs in the island are not likely to experience sediment runoff. SSTs range from 21.1 °C in winter to 28.7 °C in summer (1971–2000; Japan Meteorological Agency, 2001). The number of hermatypic coral species at Kodakara Island, based on counts from the adjacent Tanegashima and Tokunoshima islands, is estimated to be 150–200 (Veron, 1992a).

Hamanaka et al. (2015) reconstructed the Holocene reef growth history of Kodakara Island based on analysis of 7 drilling cores with 37 radiocarbon ages and delineated six sedimentary facies: (1) Facies A, *in situ* thick-plate/encrusting and tabular Acroporidae, (2) Facies B, *in situ* massive or encrusting Poritidae, (3) Facies C, *in situ* encrusting of foliaceous corals, (4) Facies D, *in situ* massive *Hydrophora* sp., (5) Facies E, reworked coral debris, and (6) Facies F, gravels from basement rock. The reef growth began at least 7.9 ka (Hamanaka et al., 2015). Three growth hiatuses occurred at ca. 5.9–5.8 ka, 4.4–4.0 ka, and 3.3–3.2 ka (Hamanaka et al., 2012).

The island is surrounded by Holocene raised reef terraces. Three raised Holocene reef terraces (Terraces I–III) formed as a result of global sea level change coupled with regional coseismic uplift (Nakata et al., 1978; Koba et al., 1979; Hamanaka et al., 2008, 2009). The highest terrace (Terrace I, dated at 2.4 ka) is 120–250 m wide and 7–10 m above present mean sea level (MSL) (Nakata et al., 1978; Koba et al., 1979; Hamanaka et al., 2008, 2009). Paleo-spurs and groove systems are present on the outer edge of the terrace.