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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.

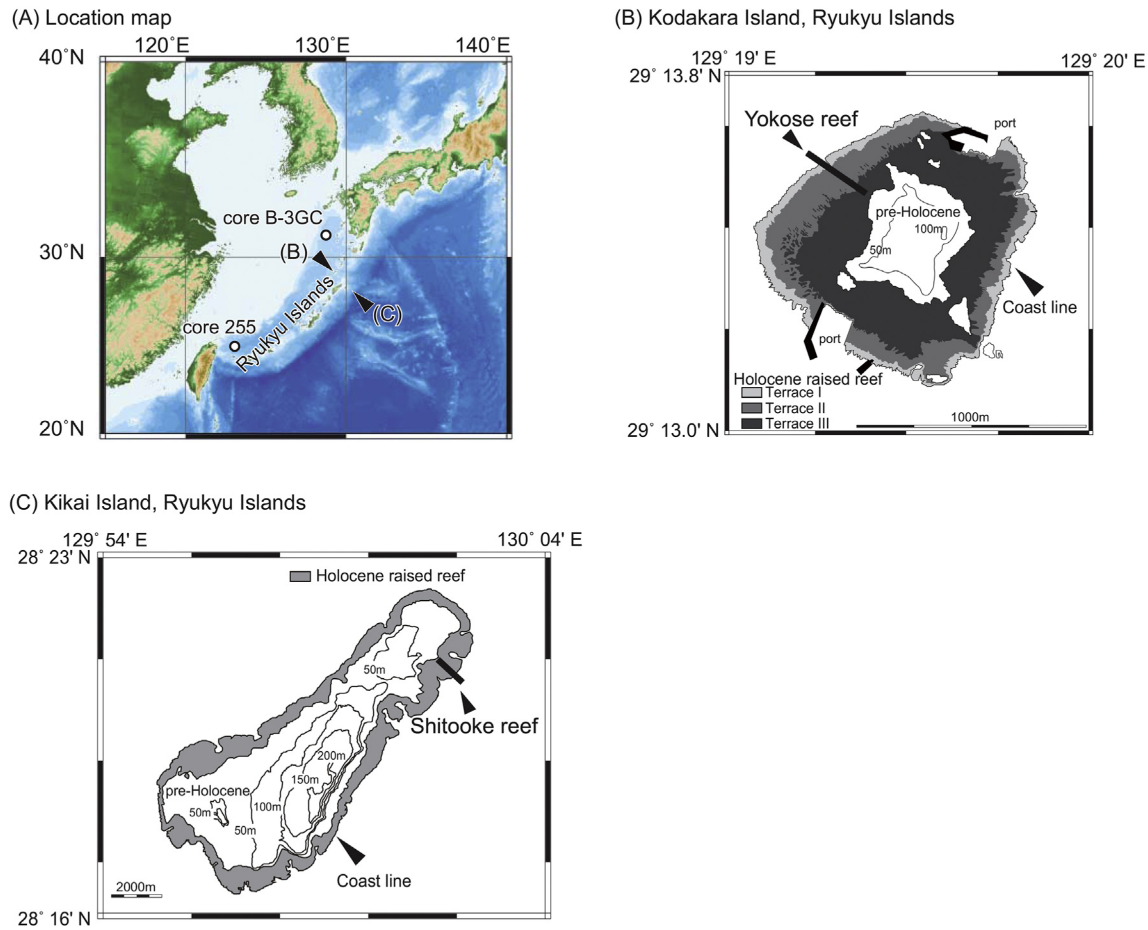

Fig. 1. (A) Map of the northwest Pacific Ocean region showing the locations of reefs investigated in this study. The two circles show the sites where marine sediment cores (core B-3GC: 31° 29′N, 128°31′E; core 255: 25° 12′N, 123°07′E) were obtained for use in reconstruction of the SSTs (Jian et al., 2000). (B) Kodakara Island, located in the northern Ryukyu Islands. The black line shows the survey transect on Yokose reef. (C) Kikai Island, located in the central Ryukyu Islands. The black line shows the survey transect on Shitooke reef.

Terrace II, dated at 1.0–0.4 ka, is 50–250 m wide and 2 m above present MSL (Nakata et al., 1978; Koba et al., 1979; Hamanaka et al., 2008, 2009). Terrace III is less than 1 m above present MSL (Nakata et al., 1978; Koba et al., 1979; Hamanaka et al., 2008, 2009). Hamanaka et al. (2015) reported that the ages of corals on Haebaru site on Terrace III range from 0.4 ka to modern.

Yokose reef, which consists of Holocene terraces and is located to the northwest of Kodakara Island, was selected for our survey (Fig. 2A–D).

2.3. Kikai Island

Kikai Island (28° 20.0′ N, 129° 59.0′ E; Fig. 1C), which has abundant corals and no major rivers, is located in the central Ryukyu Islands. The coral reefs in the island are not likely to experience sediment runoff. Seasonal SSTs range from 20.9 °C in winter to 28.5 °C in summer (1971–2000 data; Japan Meteorological Agency, 2001). A total of 220 living hermatypic coral species have been recorded at Amami Island (Veron, 1992a,b), which is adjacent to Kikai Island.

Holocene reef history of the island has been reported by previous studies (e.g., Sasaki et al., 1998; Webster et al., 1998; Ota et al., 2000; Sugihara et al., 2003). Drilled cores recorded shallowing upward sequences characterized by tabular *Acropora* spp. overlying massive *Porites* sp. and Merulinidae (Webster et al., 1998).

Kikai Island is fringed by exposed Holocene reef terraces. Four raised Holocene reef terraces (Terraces I–IV) formed as a result of global sea level change coupled with regional coseismic uplift (Ota et al., 1978). Terrace I, the highest of the Holocene reef terraces, is < 100 m wide and <10–11 m above the present MSL. Terraces II–IV are well exposed along the coastline of the island, and retain features including reef flats and distinct spur and groove systems (Sasaki et al., 1998; Webster et al., 1998; Ota et al., 2000; Sugihara et al., 2003). Terrace II is approximately 4–5 m above present MSL and is up to 200 m wide, whereas Terraces III and IV are approximately 2–3 m and 1–2 m above present MSL, respectively, and are <100 m wide (Webster et al., 1998; Ota et al., 2000; Sugihara et al., 2003). The four terraces were dated at 6.3 ka, 4.1 ka, 3.1 ka, and 1.4 ka, respectively (Sugihara et al., 2003).

Shitooke reef, located to the northeast of Kikai Island, consists of Holocene reef terraces and was chosen for investigation in this study (Fig. 2E and F). Shitooke reef is a living coral reef (Fig. 2G and H) and the coral community is dominated by *A. digitifera*, *Goniastrea retiformis*, *I. palifera*, *Acropora monticulosa*, and *Pocillopora verrucosa* (Sugihara et al., 2003). The present coral cover is 33 ± 22% (mean ± SD) (Sugihara et al., 2003).

3. Materials and methods

3.1. Topographical survey and coral observations

Topographic profiles were established along transects

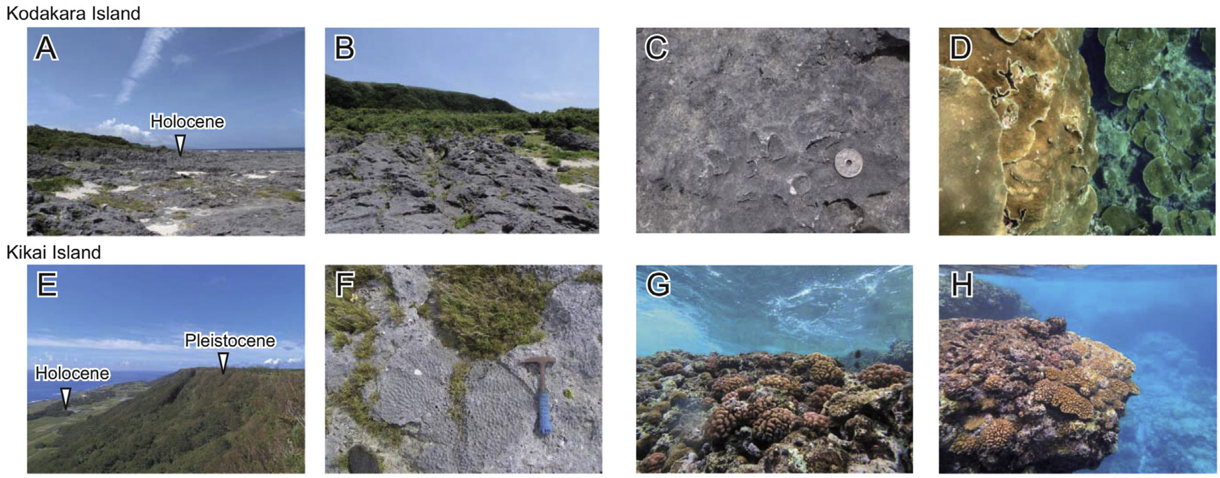

Fig. 2. Images showing the outcrops and living corals investigated in this study. For Yokose reef at Kodakara Island: (A) Holocene raised reef terraces; (B) spur and groove systems; (C) *Pocillopora verrucosa*; and (D) living encrusting *Isopora*. For Shitooke reef at Kikai Island: (E) Holocene and Pleistocene raised reefs; (F) tabular *Acropora digitifera*; (G) living *P. verrucosa*; and (H) living *Pocillopora* and *Acropora*.

perpendicular to the shoreline (the Yokose line at Kodakara Island, and the Shitooke line at Kikai Island). Elevations were recorded at 1–2 m intervals along each transect using an automatic level (Nikon AE-7) or a hand level (SOKKIA BB). The measured elevations for Kodakara and Kikai islands were calibrated to MSL using tide tables for Naze Port (Japan Meteorological Agency; see http://www.data.kishou.go.jp/kaiyou/db/tide/suisan). The topographic surveys were conducted on Kodakara Island in August 2010, and on Kikai Island in July 2009. At the survey line on Shitooke reef, Terrace I, which is the highest of the terraces, is mainly covered by vegetation and artificial structures, and consequently our observations were restricted to Terraces II, III, and IV.

Paleoecological surveys were conducted at 5–10 m intervals along the topographic profiles, along transects of 10 m length oriented perpendicular to the profiles. At Kodakara Island, 4 transects on Terrace I, 22 transects on Terraces II, and 5 transects on Terrace III were surveyed. At Kikai Island, 11 transects on Terrace II, 8 transects on Terraces III, and 9 transects on Terrace IV were surveyed. Holocene raised reef terraces are generally composed of *in situ* corals, reworked corals, and calcareous gravel and sand (e.g., calcareous algae and shells). We focused on a distribution of *in situ* corals. The line intercept transect method was used to quantitatively determine the richness and percent cover of *in situ* coral species. *In situ* fossil corals were categorized according to their growth form (e.g., tabular, massive, branching, or encrusting), and were identified to the lowest taxonomic level possible following previously reported methods (Nishihira and Veron, 1995; Wallace, 1999; Veron, 2000; Budd et al., 2012; Huang et al., 2014). The percent cover of *in situ* fossil coral species was calculated as:

$$\text{Percent cover} = \frac{\sum_{i=1}^{S} L_i}{\text{Length of transect}} \times 100$$

where L_i is the length of the ith target species, and S is the total number species along the transect. Percent cover of living corals only does not equal to that of all corals. Some portions of the colony surface were usually dead and covered with algae and other organisms. The portions of fossil coral colony on raised reef terraces were usually unclear. The current observed coral cover on the terraces may represent the maximum percentage.

3.2. Age determinations

Fossil corals from Kodakara Island were collected for U–Th dating (Shen et al., 2012). The samples were analyzed by X-ray diffraction (XRD) to confirm that the aragonite content was >99%. High-precision U–Th dating was conducted at the High-Precision Mass Spectrometry and Environment Change Laboratory (HISPEC), Department of Geosciences, National Taiwan University, Taiwan (Shen et al., 2003, 2008; 2012). Uranium–thorium isotope analyses (Shen et al., 2003) were performed using a multi-collector inductively coupled plasma mass spectrometer (MC–ICP–MS; Thermo Electron Neptune; Shen et al., 2012). The U–Th isotope contents, and the ^{230}Th ages are shown in Table 1. The half-lives of U–Th nuclides used for ^{230}Th age calculation were as reported by Cheng et al. (2013). Uncertainties in the U–Th isotope data and ^{230}Th dates are reported at the two-sigma (2σ) level, or two standard deviations of the mean ($2\sigma_m$), unless otherwise noted.

3.3. Data analysis

We assumed that the total *in situ* cover of corals on each 10 m transect length was the maximum cover for any specified time period, because the ages of all corals on the transect were not determined. Therefore, the cover data was used to represent a value for each terrace only; consequently, no temporal change in cover was detected for any terrace.

Based on pooled data for each terrace, we used the non-parametric Mann-Whitney test to assess whether there were discernible differences in total coral cover, and the cover of dominant genera and species. We compared the coral cover in the following pairs: (1) Terrace I vs. Terrace II on Yokose reef, (2) Terrace I vs. Terrace III on Yokose reef, (3) Terrace II vs. Terrace III on Yokose reef, (4) Terrace II vs. Terrace III on Shitooke reef, (5) Terrace II vs. Terrace IV on Shitooke reef, (6) Terrace II vs. the present Shitooke reef, (7) Terrace III vs. Terrace IV on Shitooke reef, (8) Terrace III vs. the present Shitooke reef, and (9) Terrace IV vs. the present Shitooke reef. The record for the present reefs is based on a report of living coral (33 ± 22%; mean ± SD) at water depths of 1–5 m on Shitooke reef (Sugihara et al., 2003). The test was performed using R software (v. 2.13.0; R Development Core Team, 2011).

Table 1
^{230}Th ages of fossil corals from Holocene raised reefs at the study site.

Sample ID	Altitude from MSL (m)	Terrace No.	Sample	Aragonite content	^{238}U (ppm)[a]	^{232}Th (ppt)	δ^{234}U (measured)[a]	^{230}Th/^{238}U (activity)[d]	^{230}Th/^{232}Th (atomic, $\times 10^{-6}$)	Age (years; uncorrected)	^{230}Th Age (years; corrected)[c,d]	$\delta^{234}U_{initial}$ (corrected)[b]
Yokose Reef, Kodakara Island												
KD-1-20 (29°13′33.85″N, 129°19′22.08″E)	4.1	Terrace I	*Acropora* sp.	100%	3.691 ± 0.003	20 ± 10	148 ± 1	0.0318 ± 0.0001	110,000 ± 60,000	3010 ± 10	2950 ± 10	148 ± 1
KD-2-70 (29°13′35.23″N, 129°19′21.07″E)	1.7	Terrace II	*Acropora* sp.	100%	3.308 ± 0.004	120 ± 10	147 ± 2	0.0209 ± 0.0001	9500 ± 700	1950 ± 10	1890 ± 10	147 ± 2
KD-3-110 (29°13′6.31″N, 129°19′20.27″E)	1.8	Terrace II	*Acropora* sp.	100%	3.461 ± 0.003	50 ± 10	149 ± 2	0.0128 ± 0.0001	1400 ± 3000	1160 ± 10	1100 ± 10	149 ± 2

Analytical errors are 2σ of the mean.
[a] $[^{238}U] = [^{235}U] \times 137.77$ (±0.11‰) (Hiess et al., 2012); $\delta^{234}U = ([^{234}U/^{238}U]_{activity} - 1) \times 1000$.
[b] $\delta^{234}U_{initial}$ corrected was calculated based on ^{230}Th age (T), i.e., $\delta^{234}U_{initial} = \delta^{234}U_{measured} \times e^{\lambda_{234} * T}$, and T is corrected age.
[c] $[^{230}Th/^{238}U]_{activity} = 1 - e^{-\lambda_{230}T} + (\delta^{234}U_{measured}/1000)[\lambda_{230}/(\lambda_{230} - \lambda_{234})](1 - e^{-(\lambda_{230} - \lambda_{234})T})$, where T is the age.
[d] Age corrections were calculated using an estimated atomic ^{230}Th/^{232}Th ratio of 4 ± 2 ppm (Shen et al., 2008).

4. Results

4.1. Topography and ages of raised reefs

Three raised terraces are exposed on Yokose reef (Kodakara Island) (Fig. 3A). Three ^{230}Th ages showed that the raised reef terraces on the reef developed at 3.0 ka for Terrace I, and 1.9 and 1.1 ka for terraces II. Terrace I, which is the highest of the terraces, is at 6–7 m above present MSL, but the survey area was limited to a width of approximately 20 m because much of the terrace is covered by vegetation. Terrace II is approximately 2 m above present MSL and 105 m wide. Terrace III is < 1 m above present MSL and is approximately 45 m wide. The ages and topographic characters are consistent with the data of Hamanaka et al. (2015).

Three raised terraces were evident on Shitooke reef (Kikai Island) (Fig. 3B). Terrace II is at 4–5 m above present MSL, but the landward survey area is limited to a width of approximately 110 m, because part of the terrace is covered by vegetation. Terrace III is 2–4 m above present MSL and is approximately 80 m wide. Terrace IV is < 2 m above present MSL, and is approximately 110 m wide. The topographic characteristics are consistent with the results of previous studies (e.g., Webster et al., 1998; Sugihara et al., 2003).

4.2. Coral cover

The total coral cover at the study sites is shown in Table 2. As shown in Table A.1, analysis of the data showed that there is a significant difference in total coral cover between Terrace I (8.0 ± 2.2%; mean ± SD) and Terrace II (20.3 ± 8.0%) at Yokose reef (Mann-Whitney test, $p < 0.05$), but no difference between Terrace II and Terrace III (20.3 ± 8.0%). However, the coral data for Terrace I was limited to the oceanward area because the landward area is covered with vegetation.

For Shitooke reef, there is a significant difference in total coral cover between Terrace II (17.9 ± 5.4%) and other sites (Terrace III: 43.2 ± 10.6%, Terrace IV: 34.6 ± 7.2%, the present-day reef: 33.4 ± 22.3%; Mann-Whitney test, $p < 0.05$), but no difference in the cover among the other comparison sites (i.e., Terrace III, Terrace IV, and the present reef). However, the data for Terrace II is limited to the oceanward area because the landward area is covered by vegetation.

4.3. Coral genera

The coral data for Terrace I on Yokose reef and Terrace II on Shitooke reef were limited due to the limited areas available. Consequently, descriptions of the genera and species (below) are limited to Terraces II–III on Yokose reef, and Terraces III–IV and the present reef on Shitooke reef.

The raised reef terraces of Yokose reef included 20 genera and 31 species of *in situ* fossil corals. Terrace II was dominated by the genera *Acropora* and *Isopora*, while Terrace III was dominated by *Acropora* and *Pocillopora* (Table 2). The cover of *Pocillopora* corals is significantly higher on Terrace III than Terrace II (Mann-Whitney test, $p < 0.05$; Table A.2), whereas there is no difference in the cover of other genera.

The raised reef terraces of Shitooke reef included 14 genera and 31 species of fossil corals. All terraces (III and IV) were dominated by *Acropora* (Table 2), but *Goniastea* was also common on the terraces. There is no significant difference in the percentage cover of any genus between Terraces III and IV (Table A.2). The cover of the genus *Isopora* was significantly greater on the present reef than on Terrace III (Mann-Whitney test, $p < 0.05$), whereas the cover of the genera *Acropora* and *Goniastrea* was significantly less

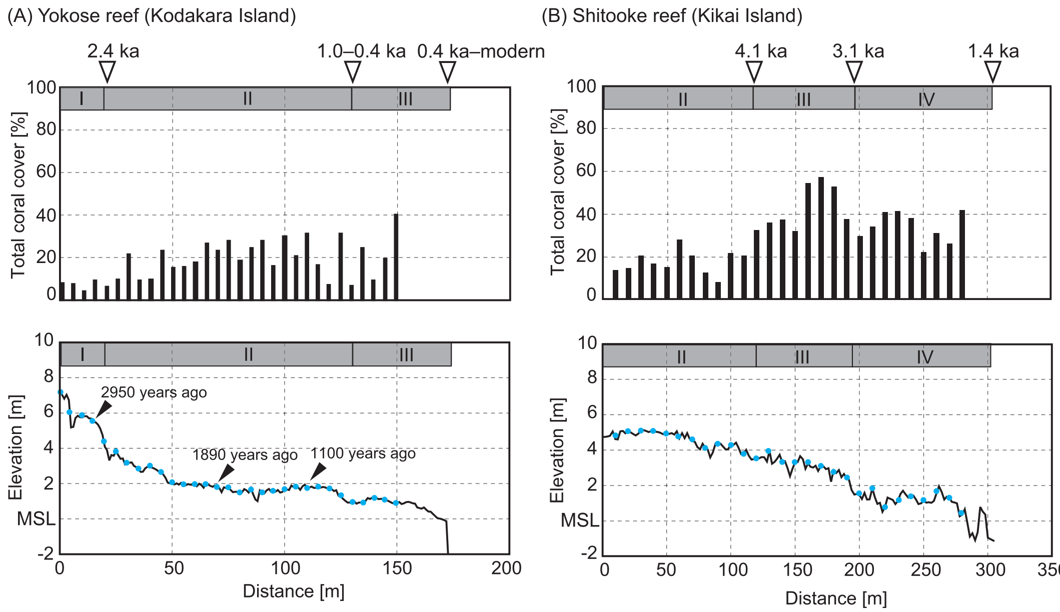

Fig. 3. Total coral cover (%) and topographic profiles for (A) Yokose reef on Kodakara Island, and (B) Shitooke reef on Kikai Island. Circles show the locations of line intercept transect surveys. Age data for Yokose reef were obtained by uranium–thorium dating. Uplift ages for Yokose reef were obtained by radiocarbon dating, based on analysis of the data of Haebaru site of Hamanaka et al. (2015). Uplift ages for Shitooke reef were obtained by radiocarbon and uranium–thorium dating based on analysis of the data of Sugihara et al. (2003). MSL: mean sea level.

Table 2
Percent cover for coral genera at the study sites.

Percent cover of genera (mean ± SD)[a]	Yokose reef, Kodakara Island			Shitooke reef, Kikai Island			
	Terrace I	Terrace II	Terrace III	Terrace II	Terrace III	Terrace IV	Modern[b]
Acropora	2.2 ± 1.4 [27.5]	7.7 ± 7.9 [37.7]	4.9 ± 4.7 [23.6]	7.8 ± 4.5 [43.5]	21.4 ± 5.2 [49.5]	13.3 ± 8.7 [38.4]	12.9 ± 15.7 [38.6]
Isopora	0.0 ± 0.0 [0.0]	7.1 ± 7.5 [34.8]	1.2 ± 2.8 [6.0]	0.9 ± 2.6 [4.8]	0.9 ± 1.9 [2.0]	0.7 ± 1.5 [1.9]	3.2 ± 2.7 [9.7]
Goniastrea	2.1 ± 1.5 [25.6]	1.7 ± 1.9 [8.3]	3.7 ± 3.8 [18.0]	2.6 ± 2.9 [14.5]	10.0 ± 6.4 [23.2]	10.8 ± 7.8 [31.3]	4.7 ± 7.7 [14.2]
Favites	2.0 ± 1.8 [24.7]	0.6 ± 1.3 [3.0]	0.0 ± 0.0 [0.0]	0.2 ± 0.8 [1.3]	3.3 ± 4.1 [7.7]	3.4 ± 2.6 [9.8]	4.0 ± 6.5 [12.0]
Pocillopora	0.2 ± 0.3 [1.9]	1.3 ± 2.4 [6.3]	10.6 ± 11.8 [51.1]	0.0 ± 0.0 [0.0]	1.3 ± 2.2 [3.0]	0.2 ± 0.2 [0.5]	2.6 ± 2.2 [7.7]
others	1.6 ± 1.4 [20.3]	2.0 ± 3.2 [9.9]	0.3 ± 0.6 [1.3]	6.4 ± 4.3 [35.9]	6.3 ± 3.3 [14.6]	6.2 ± 3.5 [18.0]	5.9 ± 8.9 [17.8]
Total	8.0 ± 2.2 [100]	20.3 ± 8.0 [100]	20.7 ± 13.4 [100]	17.9 ± 5.4 [100]	43.2 ± 10.6 [100]	34.6 ± 7.2 [100]	33.4 ± 22.3 [100]

[a] A relative cover is shown in brackets.
[b] Modern data is based on living coral cover in water depths of 1–5 m. The data from Sugihara et al. (2003).

(Mann-Whitney test, $p < 0.05$). There are no differences in coral cover for the other genera between Terrace III and the present reef. The cover of the genera *Isopora* and *Pocillopora* was significantly higher on the present reef than on Terrace IV (Mann-Whitney test, $p < 0.05$), whereas the cover of *Goniastrea* was significantly less (Mann-Whitney test, $p < 0.05$). For the other genera, there are no significant differences in cover between Terrace IV and the present reef.

4.4. Coral species

The cover of particular coral species is shown in Table A.3. At Yokose reef, Terrace II was predominantly composed of *A. digitifera*, *A. aspera*, *A. hyacinthus*, *Acropora* sp., *I. palifera*, *G. retiformis*, and *Goniastrea stelligera* (Table A.3). On Terrace III, *A. digitifera*, *A. aspera*, *Acropora* sp., *I. palifera*, *G. retiformis*, *P. verrucosa*, and *Pocillopora meandrina* were the dominant corals (Table A.3). On Yokose reef, for *Pocillopora* sp. the cover was significantly greater on Terrace III than Terrace II (Mann-Whitney test, $p < 0.05$; Table A.4), whereas there is no significant difference in cover for the other species (Table A.4).

At Shitooke reef, Terrace III was predominantly composed of *A. digitifera*, *A. robusta*, corymbose *Acropora* sp., *G. retiformis*, *G. stelligera*, and *Favites chinensis* (Table A.3). On Terrace IV, *A. digitifera*, corymbose *Acropora* sp., *G. retiformis*, *G. stelligera*, *F. chinensis*, and *Platygyra ryukyuensis* were the dominant corals (Table A.3). There were no significant differences in the cover of any species between Terrace III and Terrace IV (Table A.4). For *I. palifera*, the cover was significantly greater on the present reef than on Terrace III (Mann-Whitney test, $p < 0.05$), whereas the cover of corymbose *Acropora* sp., *G. stelligera*, and *F. chinensis* was significantly less on the present reef (Mann-Whitney test, $p < 0.05$). There is no significant difference in the cover of other species between Terrace III and the present reef. The cover of *I. palifera* and *P. verrucosa* was significantly greater on the present reef than on Terrace III (Mann-Whitney test, $p < 0.05$), but was significantly less for corymbose *Acropora* sp., *G. stelligera*, and *F. chinensis* (Mann-Whitney test, $p < 0.05$). There is no significant difference in cover for the other species between Terrace IV and the present reef.

5. Discussion

5.1. Coral cover on past reefs

Centennial-scale disturbance events have been reported for

Kodakara and Kikai Islands (Abram et al., 2001; Hamanaka et al., 2012, 2015). Hiatus events resulting from low SSTs and sea level oscillations occurred at approximately 5.9–5.8 ka, 4.4–4.0 ka, and 3.3–3.2 ka on Kodakara Island (Hamanaka et al., 2012, 2015), and in the period 3.8–3.4 ka the total coral cover decreased from 40% to 20% at Kikai Island in response to decreasing SSTs (Abram et al., 2001). However, our measured and previous reported ages (e.g., Hamanaka et al., 2012, 2015) indicate that the corals on Terrace II and Terrace III at Yokose reef represent a time range of 1.4–2.0 kyr from 2.4 ka to 1.0–0.4 ka and maximum 1.0 kyr from 1.0 to 0.4 ka to 0.4 ka–modern, respectively. Similarly, Terraces III and IV at Shitooke reef represent time ranges of 1.0 kyr from 4.1 ka to 3.1 ka and 1.7 kyr from 3.1 ka to 1.4 ka, respectively (Fig. 3). Consequently, our data indicate changes in coral cover and genera/species composition on millennial timescales, because the data are based on the age of formation of each terrace.

Based on our statistical test of coral cover on the raised terraces, there is no significant temporal change of coral cover at the study sites. The mean pristine coral cover was probably 20.3–20.7% on Yokose reef after 2.4 ka, and 34.6–43.2% on Shitooke reef after 4.1 ka. This result is consistent with reported estimates of 20–40% coral cover on terraces III and IV on Kadon reef at Kikai Island (Webster et al., 1998; Abram et al., 2001). The cover has apparently been maintained on the present Shitooke reef (33%, Sugihara et al., 2003). Millennial-scale stability of the ocean environment in the late Holocene probably helped maintain the millennial-scale coral cover at the study sites. Paleo-sea level curves show that there was a rapid sea level rise between 10 and 6 ka (Chappell and Polach, 1991; Kawana, 2006; Hongo and Kayanne, 2010a, Fig. 4A). Relative sea level rise generally promotes upward reef growth (e.g., Montaggioni, 2005), as represented by the reefs at Kodakara Island (Hamanaka et al., 2012, 2015) and Kikai Island (Webster et al., 1998; Ota et al., 2000). However, the sea level stabilized after 6 ka, and the amplitude of <2 m (e.g., Kawana, 2006): the area in this study is characterized by a tidal range of approximately 2 m. We assume that no significant changes in fossil coral cover have occurred in response to the sea level stabilization since 6 ka. Solar radiation is a primary environmental determinant of the growth of corals (Done, 2011). During the last 7 kyr, June insolation values in the region of the study sites (at latitudes 20–30°N) have gradually decreased by 34–36 W m^{-2}, and the December insolation values have gradually increased by 24–20 W m^{-2}. However, the mean annual insolation during the last 7 kyr varied by only 2 W m^{-2} (Berger and Loutre, 1991, Fig. 4B); consequently, we assume that changes in paleo-solar insolation during this time are unlikely to have affected the coral ecosystems directly. The optimal SST for coral growth is > 18 °C (Veron, 1995), and coral bleaching is reported to occur at SSTs > 29.5 °C (Kleypas et al., 1999). Reconstructed SSTs in the vicinity of our study area range from 18 to 29 °C (Jian et al., 2000; Abram et al., 2001, Fig. 4C). Low SSTs (<18 °C) occurred over short intervals at 3.8, 3.4, and 1.9 ka (Jian et al., 2000; Abram et al., 2001), but the millennial-scale SSTs have been stable.

Notably, the fossil coral cover did not apparently exceed 60%, even if the data represents the maximum cover for an assumed time period. In the northern Great Barrier Reef, a relative pristine region, the consistent modern coral cover has been >24% (De'ath et al., 2012). In the Caribbean, coral cover reached approximately 50% in the 1970s (Gardner et al., 2003). However, coral reefs have been subject to recent dramatic decrease in coral cover as a consequence of both local and global impacts (e.g., Bellwood et al., 2012; Burke et al., 2011). For example, the 1998 bleaching event reduced coral cover from 36% to 11% at a reef of Sesoko Island in the Ryukyu Islands due to elevated SSTs (Loya et al., 2001). In this context, various reef restoration strategies including coral

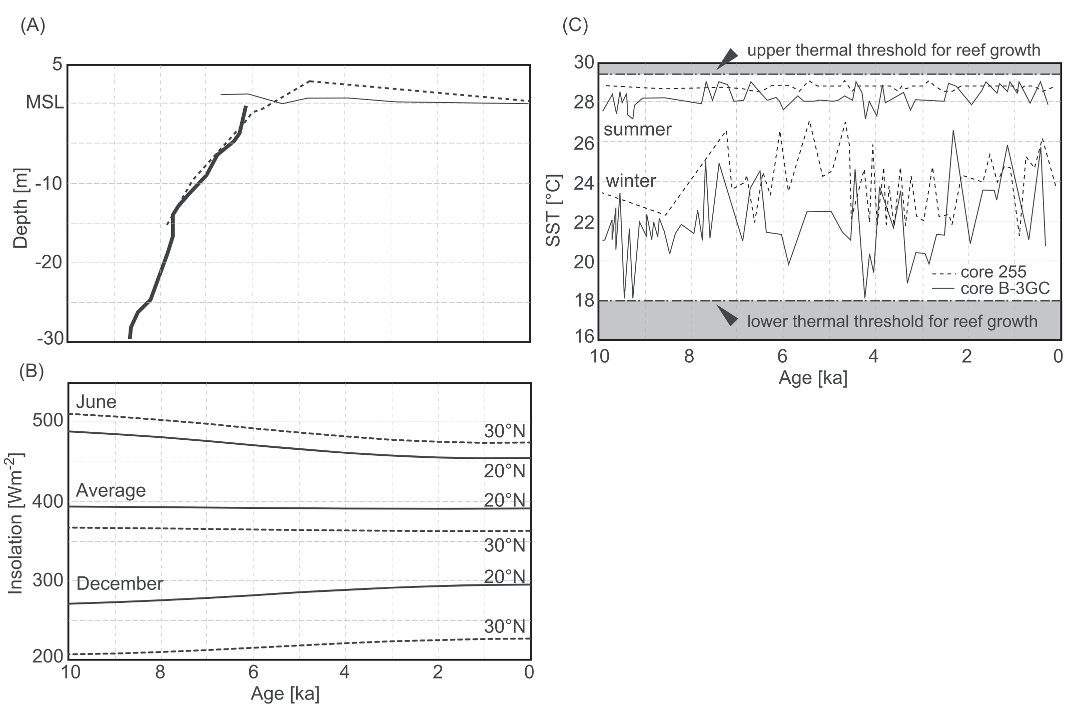

Fig. 4. Environmental factors for reef growth during the last 10 kyr. (A) Paleo-sea level curves. Solid, thin, and dashed lines show sea level curves for Papua New Guinea (derived from Chappell and Polach, 1991), Amami-oshima Island in the Ryukyu Islands (from Kawana, 2006), and Ishigaki Island in the Ryukyu Islands (from Hongo and Kayanne, 2010a), respectively. MSL: mean sea level. (B) Mid-month insolation at 20°N and 30°N, calculated by Berger and Loutre (1991). The data are archived at the NOAA National Climatic Data Center (see Orbital Variations; http://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/climate-forcing). (C) Sea surface temperatures (SSTs) derived from foraminifera records, based on data from cores B-3GC and 255 (Jian et al., 2000). Shaded bar indicates upper and lower thermal thresholds for reef growth (29.5 °C and 18.0 °C, respectively) (Veron, 1995; Kleypas et al., 1999).

transplantation have been conducted on reefs (Horoszowski-Fridman et al., 2011; Omori et al., 2016). However, knowledge of quantitative covers for coral transplantation is poorly understood. Our results imply that the need for coral cover to maintain reef ecosystem may represent 20–40%. This probably provides important information for the development of effective reef restoration plan in the future.

5.2. Dominant coral species on past reefs

The terraces were predominantly composed of *Acropora* and *Goniastrea* corals on Yokose reef after 2.4 ka, and after 4.1 ka on Shitooke reef, with *A. digitifera* and *G. retiformis* being the dominant species. These species are also dominant on the present Shitooke reef (Sugihara et al., 2003), which suggests that there is no significant change in the dominant species from 2.4 to 4.1 ka to the present. The fossil corals species are thought to represent the community composition on the reef crest–upper reef slope zone. In the Ryukyu Islands and in other reefs of the Indo-Pacific region, this zone is subject to high wave energy conditions at water depths of <10 m, and low levels of turbidity (Nakamori, 1986; Sagawa et al., 2001; Montaggioni and Braithwaite, 2009; Hongo and Kayanne, 2010b). This implies that millennial-scale environmental conditions, including wave energy and water depth, have remained stable, even if the study sites were affected by seismic uplift of several meters.

Analysis of Holocene drilled cores on Kodakara (Hamanaka et al., 2015) and Kikai Islands (Webster et al., 1998; Ota et al., 2000) indicate that the internal reefs were characterized by a significant decrease in populations of massive and encrusting corals (e.g., *Porites* and *Goniopora*) in the community, and a corresponding increase in corymbose and tabular corals, e.g., *Acropora*. The millennial-scale change in the coral community was driven principally by increasing water energy because of a decrease in habitat availability associated with Holocene sea level change (e.g., Webster et al., 1998). The present study indicates that the reef crest–upper reef slope coral community (e.g., *A. digitifera*, *I. palifera*, *G. retiformis*, and *G. stelligera*) survived under the millennial-scale variability in water energy and water depths following the Holocene sea level stabilization.

To effectively conduct reef restoration in the future, it is necessary to retrieve historical background of coral community. Investigations of Holocene raised reefs and drilled cores are robust methods for understanding the changes in biogeography of dominant corals from the past to the present. For example, *A. digitifera* is currently widely distributed in the Indo-Pacific region (Veron, 2000), but past patterns of its distribution are unclear (Hongo and Montaggioni, 2015). Our results show that this species dominated the community at Kikai Island from at least 4.1 ka to the present and at Kodakara Island from at least 2.4 ka to 1.0–0.4 ka. Sugihara et al. (2003) reported the species appeared at least 7.7 ka. This species is also observed on reefs of the Palau Islands since 7.3 ka (Hongo and Kayanne, 2011) and Ishigaki Island since 7.8 ka (Hongo and Kayanne, 2009). *A. digitifera* could be the dominant coral in the northwest Pacific from 8 ka to the present. In contrast, the species settled on the western Mauritius coast at 6 ka and the western coast of Madagascar at 1.5–1 ka (Hongo and Montaggioni, 2015). Corals are governed by biological and/or oceanographic factors. Nishikawa and Sakai (2005) reported that the number of attached *A. digitifera* planulae peaked four days following spawning. It implies that the dispersal area is relatively near the location of the parental colony. Consequently, successful region-wide dispersal of the larvae requires the maintenance of favorable oceanographic conditions over a long period of time. The region from the Palau to the Ryukyu Islands is affected by the strong Kuroshio Current, which promotes a high level of gene flow (Nakajima et al., 2010). Moreover, millennial-scale persistence of a number of *A. digitifera* may have increased the abundance of the species on present-day reefs. The presence of a number of colonies of a given species may contribute to an increase in its genetic diversity. Thus, increased genetic diversity in *A. digitifera* may increase its adaptive potential to rapid changes in environmental conditions (Ayre and Hughes, 2004).

Our field observations indicate that *G. retiformis* was a dominant coral on the raised terraces of the Shitooke and Yokose reefs, and remains one of the dominant species on the present Shitooke reef (Sugihara et al., 2003). In the Ryukyu Islands the species has been present at reefs of Ishigaki Island since approximately 6 ka (Hongo and Kayanne, 2009), Kume Island since approximately 5 ka (Takahashi et al., 1988), and Kikai Island since 7.3 ka (Sugihara et al., 2003). Although the dispersal period of the species is within one week following spawning (Connolly and Baird, 2010), the Kuroshio Current probably rapidly transports the larvae towards high latitudes in the Ryukyu Islands.

5.3. Conclusions and further research

The present study attempted to reconstruct the pristine reef conditions at two raised reef islands in the Ryukyu Islands in the northwest Pacific Ocean over the past 2.4 kyr (Kodakara Island) and 4.1 kyr (Kikai Island), based on analyses of quantitative ecological data on coral cover and genus/species composition. Various global climate changes, including increasing SST, will probably have negative effects on the genus/species composition. For example, the SSTs of the waters adjacent to the Ryukyu Islands could increase by 1.4–2.1 °C during the 21st century (Japan Meteorological Agency, 2008) and, as a result, bleaching is predicted to occur annually in this area after 2060 (Yara et al., 2009). This prediction implies that coral species will be at risk, and may be subject to large declines in the future. Therefore, various approaches have been applied to the conservation and restoration of coral reefs, including direct transplantation of juvenile and adult corals (Horoszowski-Fridman et al., 2011; Omori et al., 2016). This is considered a potential tool for the restoration of coral cover on degraded reefs. Our paleoecological results show that the mean coral cover on pristine reefs at Kodakara and Kikai islands has probably ranged from 20 to 40%, and that the reefs were predominantly characterized by *A. digitifera* and *G. retiformis*. Consequently, these data may well provide target coverage and species selection for transplantation efforts and a basic criterion for designing for MPAs and EBSA, if these reefs show evidence of decline. However, the study had some limitations, and further research is necessary.

1. The present study was restricted to millennial-scale reconstructions of coral cover. To reconstruct centennial-scale changes in coral cover, it is necessary to measure the ages of more *in situ* fossil corals along transects perpendicular to the shoreline or along transects parallel to the shoreline on raised reef terraces.
2. The present study investigated past coral reefs at Kodakara and Kikai Islands only. To understand the biogeography of communities forming pristine reefs in the Indo-Pacific region, observations of other raised reefs will be required. Other Holocene raised reefs islands have been reported in the Ryukyu Islands, including at south Okinawa Island (Kawana and Pirazzoli, 1985), Kume Island (Omoto, 1979; Koba et al., 1982), Takara Island (Koba et al., 1979), Nakanoshima Island (Nakata et al., 1978), and Yakushima Island (Nakata et al., 1978). Similarly, paleoecological surveys of other raised reefs in the Indo-Pacific region (e.g., Vatuatu: Cabioch et al., 2003) should be conducted. The

topographic features and the ages of fossil corals on these raised reefs have been documented, but detailed ecological data on coral cover and genus/species composition is lacking.

3 This study focused on the coral community of the reef crest–upper reef slope, because the fossil corals on the surface of the raised reef terraces represented this habitat. However, coral reefs can be divided into various habitats, including shallow reefs and lower reef slopes. To reconstruct genus/species coral records for such habitats, analysis using a robust method such as drilled cores is required (e.g., Ota et al., 2000; Sagawa et al., 2001; Hongo and Kayanne, 2011; Hongo, 2012). However, this method is not highly applicable to measuring coral cover. Consequently, vertical observations in artificial trenches on coral reefs should be considered (e.g., Kan et al., 1997).

4. To accurately compare fossil coral covers on raised reef terraces with live coral covers, it is necessary to examine a process of taphonomy. Coral reefs can suddenly be uplifted due to earthquakes (Kayanne et al., 2007). Field observations of the emerged corals should also be considered.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2017.08.054

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