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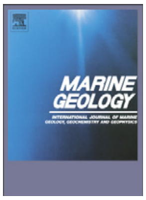

Key species of hermatypic coral for reef formation in the northwest Pacific during Holocene sea-level change

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ABSTRACT

Cores from Holocene reefs provided a growth history and species-level identification of corals and demonstrated the most important reef builders during the formation stage. This knowledge is important to determine a principle for reef formation and to provide preservation plans in the near future. A biological and sedimentological study of sediment cores recovered from the Palau Islands and Yoron Island, northwest Pacific, revealed four major facies: corymbose *Acropora*, arborescent *Acropora*, massive *Porites*, and detritus. Species-level observations show that arborescent *Acropora* (*A. muricata* and *A. intermedia*) contributed to reef growth under low- to moderate-energy conditions, whereas corymbose and tabular *Acropora* (*A. digitifera*, *A. hyacinthus*, and *A. robusta*/*A. abrotanoides*) and *I. palifera* were key species for reef formation under high-energy conditions during Holocene sea-level rise and the ensuing period of sea-level stability. Once sea level had stabilized, massive *Porites* became restricted to areas subjected to low-energy, turbid conditions. These key species are successful corals because the ecological strategy is rapid growth, determinate growth, a high degree of colony integration, strongly resistant to wave action, and rapid local dispersion via fragmentation. Moreover, the western boundary current (Kuroshio) flows along the reefs in the northwest Pacific and it is easy for key species to distribute throughout the region during the period of Holocene sea-level rise and stabilization. These features are a principle for reef formation during sea-level changes. These key species played a significant role in Holocene reef formation in the northwest Pacific; however, coral mortality, caused by climate change, has recently been widely reported. Moreover, the decrease in key species abundance in present-day reefs has been more severe than that in any other species. These geological findings have important implications regarding the appropriate use of coral transplantation and decisions regarding the optimal location and size of marine protected areas.

1. Introduction

Knowledge of coral reef growth patterns and internal facies during the Holocene has increased greatly in the last 40 years. Reefs from the Indo-Pacific region and the Caribbean have been studied so that it is now possible to determine general and regional patterns of formation, and the relationship between reef growth and corals (e.g., Cabioch et al., 1995; Macintyre and Glynn, 1976; Marshall and Davies, 1982; Montaggioni and Faure, 1997). Previous geological studies have revealed that some genera are important in terms of understanding the above topics. Although more than 200 scleractinian genera are currently found throughout the world (Veron, 2000), few played a part in reef formation during the Quaternary. For example, post-glacial reefs in the Pacific were composed mainly of corymbose and arborescent *Acropora* (e.g., Cabioch et al., 1995; Hopley and Barnes, 1985; Kayanne et al., 1993; Kennedy and Woodroffe, 2000; Marshall and Davies, 1982; Takahashi et al., 1988). Holocene reefs in the Indian Ocean also comprised mainly corymbose and arborescent *Acropora* (e.g., Camoin et al., 1997; Gischler et al., 2008; Montaggioni and Faure, 1997). Moreover, the genera *Porites* and *Pocillopora* were the main reef builders in the Hawaiian Islands and eastern Pacific (e.g., Cortés et al., 1994; Grossman and Fletcher, 2004; Macintyre et al., 1992). In the Caribbean, reefs were also composed predominantly of *Acropora* (e.g., Aronson et al., 2005; Blanchon et al., 2002; Gischler and Hudson, 2004; Hubbard et al., 2005; Macintyre, 2007; Macintyre and Glynn, 1976). Other genera (e.g., *Favia*, *Favites*, *Goniastrea*, *Platygyra*, and *Montastrea*) were observed in the Indo-Pacific region during the reef-formation stage (Cabioch et al., 1995; Camoin et al., 2004; Marshall and Davies, 1982; Montaggioni and Faure, 1997).

The genus *Acropora* is an especially important scleractinian taxa on reefs throughout much of the Pacific Ocean and the Caribbean. Although the genera *Pocillopora* and *Porites* are represented by fewer than 10 species and approximately 80 species, respectively, *Acropora* is notable as the most diverse coral, with over 200 species (Veron, 2000). In the Caribbean, the present day and the Holocene reefs were dominated by *Acropora palmata* and *Acropora cervicornis* (e.g., Aronson et al., 2005;

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Blanchon et al., 2002; Gischler and Hudson, 2004; Hubbard et al., 2005). In the Indo-Pacific region, the distribution of *Acropora* species in the present ocean has been intensely studied (e.g., Veron, 1986, 2000; Wallace, 1999), but reconstructions of reef growth history are usually based on data derived from growth forms, genera, and combinations of certain species. For example, the Holocene reef at One Tree Reef, Great Barrier Reef, was composed of corymbose and arborescent *Acropora* (Marshall and Davies, 1982), but species-level identification remains to be performed. In Vanuatu, reefs were dominated by several *Acropora* species, among other corals (*Porites*, *Astreopora*, and *Montipora*), during the past 23,000 years (Cabioch, 2003), although the relationship between species patterns and reef growth remains unknown. Such results have been reported throughout the Indo-Pacific region (e.g., Cabioch et al., 1995; Camoin et al., 1997; Kan and Kawana, 2006); consequently, the distribution patterns of species during past reef formation remains poorly understood.

Johnson et al. (2008) proposed that species diversity was not an important control on reef growth in the Caribbean. Hongo and Kayanne (2010b) also showed that species diversity is not a prerequisite in terms of Holocene reef growth in the Indo-Pacific and the Caribbean and this study indicated that few species are important for reef growth. For example, at Ishigaki Island in the Ryukyu Islands, the reef consisted mainly of several *Acropora* species (*A. digitifera* and *A. hyacinthus*) and other species during the period of Holocene sea-level change (Hongo and Kayanne, 2009). At Kikai Island, the Holocene reef also comprised corymbose and tabular *Acropora* (*A. digitifera*, *A. hyacinthus*, and *A. gemmifera*) and *Isopora palifera* (Ota et al., 2000; Webster et al., 1998). In the Caribbean reefs, reefs were composed of robust and arborescent *Acropora* (*A. palmata* and *A. cervicornis*) during the Holocene (Blanchon et al., 2002; Gischler and Hudson, 2004; Hubbard et al., 2005).

Moreover, the species-level records from these fossil corals suggest that the above corals are likely to be key species for reef formation in the near future. These records are valuable in terms of coral preservation, including the designation of marine protected areas (MPAs) and the selection of appropriate species for transplantation (Dizon and Yap, 2006; Edwards and Clark, 1998; Lindahl, 2003; Soong and Chen, 2003) to address the increasing decline in coral reefs caused by climate change and human impacts (Bellwood et al., 2004; Gardner et al., 2003; Hughes et al., 2003). For example, *Acropora* has been severely affected by coral bleaching events (Loya et al., 2001) and this genus shows a high degree of endemism; consequently, the loss of *Acropora* species would cause a decline in reef development in the Indo-Pacific and the Caribbean.

In reefs of the northwest Pacific, bio-lithological descriptions and radiometric dates have been obtained from numerous drilling cores recovered since the 1970s and observations of submarine-trench walls have revealed the detailed internal structure of reefs (Table 1). Data on reefs of the northwest Pacific are available from the Palau Islands (Kayanne et al., 2002), Ishigaki Island (Hongo and Kayanne, 2009; Yamano et al., 2001, 2003), Kikai Island (Konishi et al., 1978, 1983; Ota et al., 2000; Webster et al., 1998), Yoron Island (Yonekura et al., 1994), and other reefs (e.g., Hamanaka et al., 2008; Kan et al., 1991, 1995, 1997; Takahashi et al., 1988). However, little is known of the reef builder in other reefs during the Holocene because these data are restricted to genera-level observations, with the exception of Kikai Island (28°20′N, 130°00′E) and Ishigaki Island (24°25′N, 124°10′E). The purpose of the present study is to identify the Holocene species-level record from the Palau Islands (7°24′N, 134°21′E) and Yoron Island (27°02′N, 128°26′E) in the Ryukyu Islands, northwest Pacific and to identify the key species for reef formation and for preservation plans in the near future.

2. Reef sites and methods

2.1. Palau Islands

The Palau Islands consist of a number of volcanic and limestone islands (Fig. 1). The Ngemelis barrier reef (7°24′N, 134°21′E) is located west of Babeldaob Island, which is subjected to seasonal winds, including a northeast trade wind from November to May and south to southwest wind from June to October (Wolanski and Furukawa, 2007). The island is exposed to wintertime swell; however, the reef is protected by a northeasterly wind during this period, meaning that it is considered a moderate- to low-energy reef. The average sea-surface temperature (SST) in this area is 28–30 °C (Morimoto et al., 2002). The tide is semidiurnal with a range of 1.5 m at spring tide, and the mean low-water spring tide is 1.1 m below mean sea level (MSL) (NOAA, 2002).

The Ngemelis barrier reef is 1–3 km wide. This topographically well-developed barrier reef contains a distinct lagoon, reef flat, and reef slope. The lagoon, 15 km wide and with a maximum depth of 50 m, separates the island from the reef flat (Kayanne et al., 2002). Many patch reefs in the lagoon reach the sea surface, ranging in diameter from tens of meters to several kilometers. The reef flat is ~1600 m wide and is 1 m below MSL. The reef flat consists of a reef crest and sand flat. The reef crest, which occurs as a topographic high along the reef margin, is emergent during low tide. The seaward side of the reef flat is terminated at the reef slope, which slopes steeply toward the outer ocean.

The Palau Islands are situated in an area with high species diversity and are characterized by ~70 genera of hermatypic coral and ~400 species (Yukihira et al., 2007). A typical coral community of the western reef crest at Babeldaob Island consists of *A. digitifera* and other *Acropora* colonies, whereas *Porites* sp., arborescent *Acropora*, and *Pavona clavus* are the dominant corals in the lagoon (Yukihira et al., 2007). Kayanne et al. (2002) conducted a biological survey of the Ngemelis barrier reef in 1991, recording 183 coral species representing 42 genera. The most common species on the lagoon patch reefs (those which made up 30–80% of coral coverage) were *Porites lutea*, *P. rus*, and *P. cylindrica*. At the reef crest, the highest coral coverage (approximately 30%) and richness were found for corymbose *A. digitifera*; also abundant were corymbose *A. hyacinthus* and massive *P. lutea*, among other corals (*Montipora*, *Psammocora*, *Astreopora*, *Goniastrea*, and *Fungia*). The reef crest on the outer-ocean side was composed of *A. robusta* and *A. irregularis*, and other encrusting and massive corals (*Montipora* and *Goniopora*), which had coverages of 4–6%. On the sand flat, the dominant species were arborescent corals (*Acropora austera* and *Acropora muricata*), corymbose coral (*A. gemmifera*), massive corals (*Goniastrea*, *Pavona*, and *Favites*), and *P. lutea*. However, after an extensive bleaching event in 1998, the reef crest was replaced by algae and massive *Porites* (Bruno et al., 2001; Golbuu et al., 2007; Kayanne, 2007).

2.2. Yoron Island in the Ryukyu Islands

The Ryukyu Islands extend between the Kyusyu Islands and Taiwan, along which the Kuroshio runs. Yoron Island (27°02′N, 128°26′E), located north of Okinawa Island (Fig. 1), is subjected to seasonal winds: northwesterly to northerly monsoonal winds in winter and south-southwesterly winds in summer (data from the Japan Meteorological Agency; see http://www.data.jma.go.jp/obd/stats/etrn/index). The SST is 21–28 °C (Japan Meteorological Agency; see http://www.data.kishou.go.jp/kaiyou/db/kaikyo/dbindex.html). The tide is semidiurnal with a range of 1.6 m at spring tide, and the mean lower low spring tide is 1.1 m below MSL (Japan Coast Guard, 2007).

Kurohana reef, located on Yoron Island, consists of distinctly zoned landforms, comprising a reef flat (shallow lagoon and reef crest) and reef slope (Nakai, 2007; Yonekura et al., 1994). The shallow lagoon (2–5 m deep) is situated between the reef crest and the shore. The reef crest, which forms a topographic high along the reef margin, is 100–150 m wide and is emergent during low tide. The reef slope is characterized by spur and groove systems that extend 250 m seaward to a depth of 20 m.

Yoron Island contains ~200 coral species (Nishihira and Veron, 1995). In 1980–1981, the shallow lagoon was covered by massive

Table 1
Summary description of Holocene reefs of the western Pacific.

Reef location	Number of cores	Thickness of Holocene sequence	Timing of initial reef growth	Main reef builder	Reference
1. Sekisei reef (24°15′N, 124°06′E)	3 cores	21.0 m	8520 cal. years BP	Genera-level identification Reef crest: corymbose, tabular, and encrusting *Acropora* with associated massive *Porites* sp. and *Goniastrea* sp. patch reef: arborescent *Acropora*	Kan and Kawana (2006)
2. Ishigaki Island					
Tonoshiro reef (24°19′N, 124°10′E)	Submarine-trench wall	>5 m	>4430 cal. years BP	Genera-level identification Reef crest: corymbose and tabular *Acropora* Shallow lagoon: allochthonous coral and detritus	Yamano et al. (2003)
Kabira reef (24°29′N, 124°08′E)	8 cores	>7 m	>6040 years BP	Genera-level identification Reef crest: corymbose, tabular, and encrusting *Acropora* Shallow lagoon: *Motipora digitata*, allochthonous corals, and detritus	Yamano et al. (2001)
Ibaruma reef (24°30′N, 124°18′E)	4 cores	22.0 m	7820 cal. years BP	Species-level identification Reef crest: corymbose and tabular *Acropora* (*A. digitifera* and *A. hyacinthus*) and other corals (*Montastrea curta*, *Goniastrea retiformis*, *Platygyra ryukyuensis*, and *F. stelligera*) Shallow lagoon: detritus	Hongo and Kayanne (2009)
3. Okinawa Island					
Gushichan reef (26°07′N, 127°45′E)	7 cores	18.0 m	7650 years BP	Genera-level identification Reef flat: encrusting and massive corals (*Goniopora*, *Porites*, and *Favites*) and corymbose and tabular *Acropora*	Kawana and Kan (1996, 2002)
4. Tonaki Island (26°22′N, 127°08′E)	Submarine-trench wall	>8 m	>4960 years BP	Genera-level identification Reef crest: corymbose and tabular *Acropora* Shallow lagoon: arborescent *Acropora*, allochthonous corals, and detritus	Kan et al. (1997)
5. Kume Island (26°21′N, 126°43′E)	13 cores	10 m	7380 years BP	Genera-level identification Reef crest: corymbose and tabular *Acropora* with associated *G. retiformis* and *Goniastrea edwardsi* Shallow lagoon: arborescent *Acropora*, allochthonous corals, and detritus	Takahashi et al. (1988) Kan et al. (1991)
6. Minna Island (26°39′N, 127°49′E)	Submarine-trench wall	>3 m	>5160 years BP	Genera-level identification Reef crest: corymbose and tabular *Acropora* and arborescent *Acropora*	Kan and Hori (1993)
7. Okinoerabu Island (27°20′N, 128°34′E)	Submarine-trench wall	10.9 m	7050 years BP	Genera-level identification Reef flat: corymbose and tabular *Acropora*, tabular *Montipora*, and branching *Pocillopora*	Kan et al. (1995)
8. Kikai Island					
Nakaguma reef (28°20′N, 129°58′E)	19 cores	23.5 m	8530 years BP	Species-level identification Reef flat: massive *Porites* spp. (*P. lutea*, *Porites lobata* or *Porites australiensis*) and corymbose and tabular *Acropora* (*A. hyacinthus* and *Acropora monticulosa*) and *I. palifera* with associated massive corals (*F. pallida, Leptoria phrygia, Goniastrea, Favites, Platygyra, and Montastrea*)	Konishi et al. (1978, 1983) Webster et al. (1998)
Shidooke reef (28°21′N, 130°02′E)	5 cores	25.9 m	9900 years (^{230}Th/^{234}U)	Species-level identification Reef flat: corymbose and tabular *Acropora* (*A. digitifera*, *A. hyacinthus*, and *Acropora gemmifera*) and *Isopora palifera* with associated massive corals (*Favia speciosa, Favia pallida, Favites chinensis, G. retiformis, Panova minuta, P. damicornis*, and *Pocillopora verrucosa*), allochthonous corals, and detritus	Ota et al. (2000)
9. Kodakara Island (29°13′N, 129°19′E)	7 cores	>14.0 m	Unknown	Genera-level identification Reef flat: corymbose, tabular and encrusting *Acropora*, massive *Porites*, and faviidae	Hamanaka et al. (2008)
10. Mage Island (30°46′N, 130°51′E)	4 cores	2.5–3.9 m	6500 cal. years BP	Genera-level identification Reef flat: corymbose and tabular *Acropora* and encrusting corals shallow lagoon: allochthonous corals and detritus	Kan et al. (2005)

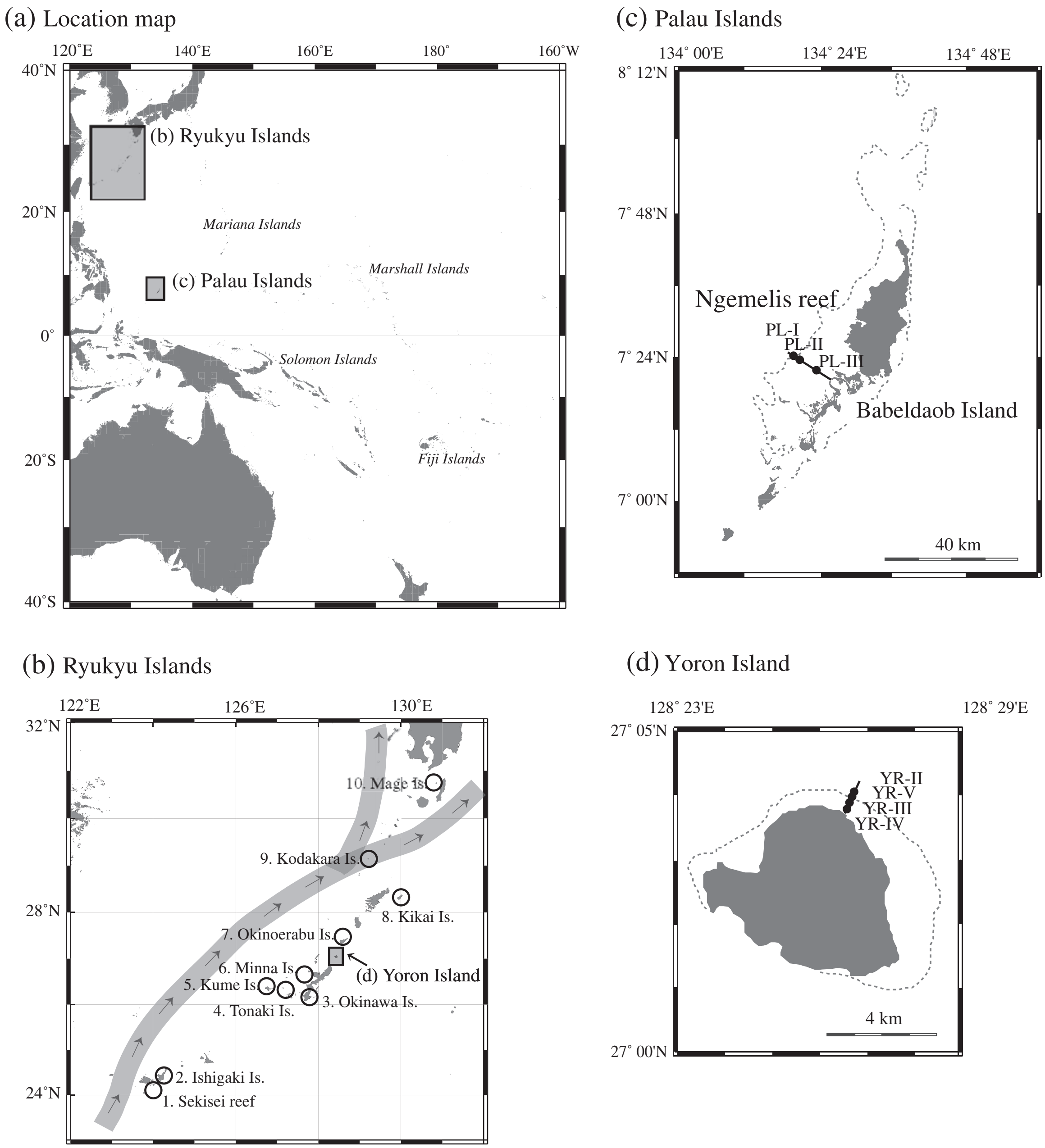

Fig. 1. (a) Location of the study area (Palau Islands and Yoron Island). (b) Map of the Ryukyu Islands, showing the location of Yoron Island and the reef sites analyzed in the present study. Solid line indicates schematic paths of the Kuroshio Current. (c) Map showing the Palau Islands and (d) the Yoron Island. Solid lines show the locations of transects along which water depth was surveyed. Black circles indicate the locations of drill sites (PL-I, PL-II, and PL-III in Palau Islands and YR-II, YR-III, YR-IV, and YR-V in Yoron Island).

corals (*P. cylindrica* and *P. lutea*), branching corals (*A. muricata* and *Montipora digitata*), and the reef crest (Nakai, 2007). The reef edge is covered with algae, encrusting coral (*Pocillopora*), massive corals (*Porites*), and *Montipora* (Yonekura et al., 1994).

2.3. Cores and radiocarbon age data

Three deep cores (PL-I, PL-II, and PL-III; 66 mm in diameter) were recovered from Ngemelis reef in the Palau Islands in 1991 (Kayanne et al., 2002). PL-I and PL-II were recovered from the reef crest and sand flat, respectively, whereas PL-III was recovered from a patch reef in the lagoon. These cores were between 25 and 30 m long, penetrating the Pleistocene reef. Cores were recovered using a rotary system with oil feed drilling system (Toho D-O type). The drill system was composed of a boring machine, a drilling pump, and drilling strings. The piston displacement of engine is 5590 W. The maximum exhaust amount of water pump is 6.0×10^{-2} m^3/min. The drilling strings consisted of core barrel, casing (88 mm in diameter), drill bit, and sediment tube. The core barrel and casing provided much better performance of high recovery. In operation, working core barrel and casing were fitted with boring machine. Before core barrel became full with sample, the drill was stopped. After pulling the core barrel to the surface, the core was kept in a box. Because the drilling system was designed for all core drilling, the average recovery varied from 61 to 77% (Table 2). On Holocene Reefs, PL-I core was characterized by high recovery (77%) because the drilling site consisted of consolidated reef crest. However, PL-II and PL-III cores were of low recovery because the composition of the lower part of each core included sand and gravel.

On Yoron Island, shallow drilling cores (1.8–3.4 m long; Table 2) with a diameter of 42 mm were obtained from four holes (YR-II, YR-III, YR-IV, and YR-V) at Kurohana reef during 1983–1984 (Yonekura et al., 1994). Three of the cores (YR-II, YR-III, and YR-V) were recovered from

Table 2
Details of drilling cores recovered from the Palau Islands and Yoron Island.

Core ID	Length (m)	Thickness of Holocene sequence (m)	Depth below MSL (m)	Recovery (%)[a]
Palau Islands				
PL-I	25.0	15.0	− 1.2	77
PL-II	25.0	16.0	–1.4	64
PL-III	30.0	23.0	–1.5	61
Yoron Island				
YR-II	1.8	1.8	–0.4	99
YR-III	3.2	3.2	–0.5	79
YR-IV	1.5	1.5	–0.3	93
YR-V	3.8	3.8	− 0.5	98

[a] Indicates that the number is for Holocene reefs.

the reef crest, while YR-IV was recovered from the shallow lagoon. Cores were recovered using the HIPAC-CDS-2 drilling system (Ishii and Kayanne, 1986). The drill was composed of a boring machine, a drilling pump, and drilling strings. The piston displacement of engine is 63.1 cm^3 and 2900 W. The maximum exhaust amount of water pump is 3.4×10^{-2} m^3/min. The drilling strings consisted of core barrel, drill bit, and sediment tube. The double core barrel provided much better operation of high recovery. After pulling the core barrel to the surface, the bit, core shell coupling, outer core tube, and inner core tube were detached, and the core sample was drawn from the inner tube. The core was kept in an acryl tube, with thin parting strips to keep each position of core from the adjacent length. Because the drilling system is for all core drilling, the average recovery varied from 79 to 99% (Table 2).

A total of 19 samples from the Palau Islands were analyzed to obtain calibrated radiocarbon ages (Kayanne et al., 2002), and 10 coral samples from Yoron Island were analyzed to obtain conventional radiocarbon ages (Yonekura et al., 1994); consequently, these latter ages were calibrated to calendar years using the calibration program CALIB Rev. 5.0 (Stuiver and Reimer, 1993; Stuiver et al., 2005) and the marine calibration dataset Marine 04 (Hughen et al., 2004), assuming a marine reservoir effect of –400 years (Stuiver and Braziunas, 1993; Stuiver et al., 1986). All the radiocarbon ages are listed in Table 3.

2.4. Biological and sedimentological analyses

The cores were subjected to biological and sedimentological analyses. Each core sample was sliced longitudinally or laterally into two roughly equal halves using a water-cooled saw. The nature and reliability of criteria used to identify *in situ* corals vary according to growth orientation. The criteria are similar in principle to Montaggioni and Faure (1997). The concave surfaces of corymbose and tabular corals are usually orientated upward during growth, such that there is generally little doubt about the growth orientation. In contrast, massive corals may re-acquire a normal growth orientation after displacement. Moreover, an abrasion of tip of branching coral is usually important to identify growth position. Therefore, *in situ* corals were identified based on a combination of criteria: the upward orientation of well-preserved corallites and a lack of severe surface abrasion and rounding. Coral samples were identified to the lowest possible taxonomic level, following Nishihira and Veron (1995), Veron (1986, 2000), and Wallace (1999).

On Yoron Island, Yonekura et al. (1994) reported the growth forms of coral species and their thickness from cores at Kurohana reef. For example, massive *Acropora* (80–140 mm thick) and branching plates of *Acropora* (60–80 mm thick) were observed. Our observations indicate that these corals have many primary branches that can be traced along an axis from the center of the colony to the tip of the branch. Consequently, these skeletal characteristics generally indicated

Table 3
Radiocarbon ages of corals from the Palau Islands and Yoron Island.

Sample ID	Depth below MSL (m)	Coral type	Conventional ^{14}C age (years BP ± 1σ)	Calibrated ^{14}C age (cal. years BP; 2σ range is shown in parentheses)	Laboratory code
Palau Islands*					
PL-I-3	− 1.8	Massive *Porites* sp.	3950 ± 60	3920 (3773–4125)	JGS-438
PL-I-8	− 2.5	Algal crust	5870 ± 90	6280 (6076–6490)	JGS-415
PL-I-26	− 4.4	*Acropora digitifera*	6600 ± 90	7150 (6894–7310)	JGS-412
PL-I-43	− 6.8	*Acropora digitifera*	6720 ± 80	7250 (7068–7413)	JGS-416
PL-I-67	− 12.0	*Acropora* sp. cf. *A. muricata*/*A. intermedia*	6860 ± 80	7390 (7225–7521)	JGS-417
PL-I-79	− 15.1	Massive *Porites* sp.	7830 ± 90	8310 (8092–8481)	JGS-413
PL-II-11	− 2.0	Massive *Porites* sp.	modern	modern	JGS-432
PL-II-33	− 5.0	Massive *Porites* sp.	2700 ± 60	2350 (2276–2642)	JGS-414
PL-II-49	− 9.3	*Montipora sp.*	4400 ± 110	4530 (4264–4834)	JGS-429
PL-II-58	− 12.2	*Acropora* sp. cf. *A. muricata*/*A. intermedia*	5580 ± 70	5940 (5817–6173)	JGS-430
PL-II-78	− 15.3	*Acropora* sp. cf. *A. muricata*/*A. intermedia*	6870 ± 90	7400 (7216–7542)	JGS-418
PL-III-6	− 3.0	Massive *Porites* sp.	520 ± 60	140 (1–259)	JGS-421
PL-III-8	− 3.9	Massive *Porites* sp.	570 ± 60	250 (28–309)	JGS-442
PL-III-11	− 5.9	Massive *Porites* sp.	4440 ± 70	4580 (4430–4802)	JGS-422
PL-III-17	− 9.6	Massive *Porites* sp.	4970 ± 90	5300 (5038–5533)	JGS-423
PL-III-25	− 13.8	Branching *Porites* sp.	5610 ± 80	5980 (5840–6213)	JGS-424
PL-III-34	− 17.6	Massive *Porites* sp.	6390 ± 80	6850 (6672–7092)	JGS-425
PL-III-41	− 22.6	*Acropora* sp. cf. *A. muricata*/*A. intermedia*	7380 ± 80	7830 (7669–7994)	JGS-426
PL-III-45	− 24.6	Massive *Porites* sp.	7530 ± 80	7970 (7827–8167)	JGS-427
Yoron Island**					
YR-II-1	− 0.7	*Acropora hyacinthus?*	2875 ± 80	2580 (2366–2786)	JGS-145
YR-II-2	− 0.9	*Isopora palifera*	2860 ± 60	2580 (2419–2749)	JGS-360
YR-II-3	− 2.2	*Acropora digitifera*	3300 ± 90	3130 (2892–3358)	JGS-146
YR-III-1	− 0.9	*Acropora hyacinthus*	3600 ± 80	3510 (3318–3699)	JGS-362
YR-III-2	− 2.0	*Isopora palifera*	4670 ± 90	4650 (4674–5224)	JGS-147
YR-III-3	− 3.6	*Acropora digitifera*	4760 ± 90	5050 (4824–5271)	JGS-148
YR-V-1	− 0.9	*Isopora palifera?*	3230 ± 90	3060 (2820–3299)	JGS-158
YR-V-2	− 2.3	*Isopora palifera?*	4960 ± 80	5260 (5034–5490)	JGS-365
YR-V-3	− 2.7	Corymbose *Acropora* sp.	4880 ± 80	5190 (4951–5423)	JGS-363
YR-V-4	− 3.0	Corymbose *Acropora* sp.	5260 ± 100	5650 (5424–5880)	JGS-246

*Data from Kayanne et al., (2002).
**Data from Yonekura et al., (1994).

corymbose and tabular *Acropora*. Moreover, in the case that a coral was characterized by a branch of ~10 mm in diameter and up to 30 mm long, the coral was identified as *A. digitifera* (Wallace, 1999). Based on the findings of Yonekura et al. (1994), the reef was identified as being dominated by encrusting *Acropora*. According to our observation, the skeletal characteristics included thick branches with multiple axial corallites and thus the coral was *I. palifera*, which is the most common and widespread *Isopora* species.

On Palau Islands, Kayanne et al. (2002) reported that the Ngemelis barrier reef contained abundant branching *Acropora* (6–15 mm long) and short, robust branching *Acropora* (8–15 mm long). The authors identified the corals as *A. digitifera* and *A. humilis*; however, *A. humilis* is generally characterized by a size of 10–30 mm in diameter and up to 60 mm long (Wallace, 1999). The present observations reveal that the corals from the cores were characterized by a branch of ~10 mm in diameter and usually up to 30 mm long, and other corals that are more than 30 mm in diameter with evenly distributed radial corallites and indistinct axial corallites; thus the species are identified as *A. digitifera* and *A. robusta*/*Acropora abrotanoides*, respectively.

3. Results

3.1. Bio-sedimentological units of the Palau Islands and Yoron Island

Twelve biological and sedimentological units (Units 1–12) were observed in the analyzed cores from Ngemelis reef in Palau Islands. In Yoron Island, seventeen biological and sedimentological units (Units 13–29) were observed in the cores. The detailed description and the internal structures are shown in Table 4 and Fig. 2, respectively. Coral species list in the cores is shown in Table 5. Below, each of the cores is summarized in turn.

PL-I core: this reef-crest core is composed mainly of *in situ* corals and contains four sedimentological units (Units 1–4). PL-II core: this sand-flat core is divided into three units (Units 5–7). PL-III

Table 4
Main characteristics and distribution of sedimentary units, and distribution and paleoenvironmental interpretation of facies observed at the study sites.

Facies	Unit	Characteristics	Distribution	Environmental conditions
Facies corymbose *Acropora*	Unit 4	*In situ* corymbose and tabular *Acropora* (*A. digitifera*) and robust *Acropora* (*A. robusta*/*A. abrotanoides*) with associated arborescent *Acropora* and encrusting calcareous algae	PL-I core (6.0–0 m)	Water depth of 0–7 m, high energy, low turbidity, and reef crest and upper reef slope
	Unit 13	*In situ* corymbose and tabular *Acropora* (*A. digitifera*) and *I. palifera*	YR-II core (1.8–1.5 m)	
	Unit 14	*Acropora* sp. and *Pocillopora* sp. fragments	YR-II core (1.5–1.0 m)	
	Unit 15	*In situ* corymbose and tabular *Acropora* (*A. digitifera* and *A.hyacinthus*) and *I. palifera* with associated encrusting calcareous algae	YR-II core (1.0–0.5 m)	
	Unit 16	*Acropora* sp. and *Pocillopora* sp. fragments	YR-II core (0.5–0 m)	
	Unit 18	*In situ* corymbose corals (*Acropora* sp.), *I. palifera*, and *P. damicornis* with associated encrusting calcareous algae	YR-V core (2.8–1.8 m)	
	Unit 19	*Acropora* sp. and *Pocillopora* sp. fragments	YR-V core (1.8–1.3 m)	
	Unit 20	*In situ* corymbose *Acropora* and *I. palifera* with associated *Cyphastrea* sp and encrusting calcareous algae	YR-V core (1.3–0.5 m)	
	Unit 21	*Acropora* sp. and *Pocillopora* sp. fragments	YR-V core (0.5–0 m)	
	Unit 25	*In situ* corymbose and encrusting corals (*A. digitifera* and *Montipora* sp.) with associated encrusting calcareous algae	YR-III core (1.6–1.0 m)	
	Unit 26	*Acropora*, *Pocillopora*, and *Montipora* fragments	YR-III core (1.0–0.5 m)	
	Unit 27	*In situ* corymbose and tabular *Acropora* (*A. digitifera* and *A. hyacinthus*)	YR-III core (0.5–0 m)	
Facies arborescent *Acropora*	Unit 1	Arborescent *Acropora* (*A. muricata*/*A. intermedia*) with associated massive *Porites* fragments	PL-I core (15.0–11.5 m)	Water depth of 0–20 m, low to moderate energy, low turbidity, and inner reef slope or leeward reef slope
	Unit 2	Arborescent *Acropora* (*A. muricata*/*A. intermedia*) with associated *P. damicornis* fragments and encrusting calcareous algae	PL-I core (11.5–9.5 m)	
	Unit 3	Arborescent *Acropora* (*A. muricata*/*A. intermedia*) and *Halimeda* fragments	PL-I core (9.5–7.0 m)	
	Unit 8	*In situ* arborescent *Acropora* (*A. muricata*/*A. intermedia*) with associated coral fragments (massive *Porites*) and sand (*Halimeda* and benthic foraminifera)	PL-III core (23.0–16.5 m)	
	Unit 9	*In situ* arborescent *Acropora* (*A. muricata*/*A. intermedia*) with associated *in situ* massive *Porites*	PL-III core (16.5–12.0 m)	
	Unit 10	*In situ* arborescent *Acropora* (*A. muricata*/*A. intermedia*) with associated coral fragments (*Porites* sp. and *Lobophyllia* sp.)	PL-III core (11.0–8.0 m)	
Facies massive Porites	Unit 7	*In situ* massive *Porites* sp. with associated *H. coerulea* fragments	PL-II core (5.0–0 m)	Water depth of 0–5 m, low energy, high turbidity, and shallow lagoon or lagoon
	Unit 11	*In situ* massive *Porites* sp.	PL-III core (8.0–4.5 m)	
	Unit 12	*In situ* massive *Porites* sp.	PL-III core (4.5–0 m)	
	Unit 29	*In situ* massive *Porites* sp.	YR-IV core (0.5–0 m)	
Facies detritus	Unit 5	Allochthonous coral fragments (arborescent *Acropora* sp.) and detritus sediments (sand, foraminifera tests, and *Halimeda* fragments) with associated *in situ* coral (*Goniastrea* sp.)	PL-II core (16.0–10.0 m)	Low energy, high turbidity, and shallow lagoon or lagoon
	Unit 6	Allochthonous coral fragments (arborescent *Acropora* sp.) and detritus sediments (*Halimeda* fragments, gastropods, echinoid debris, and benthic foraminifera tests) with associated *in situ* coral (*Montipora* sp.)	PL-II core (9.0–6.0 m)	
	Unit 17	Allochthonous coral fragments (*Acropora* sp. and P. *damicornis*) and sand with associated few *in situ* corals (*I. palifera*)	YR-V core (3.8–2.8 m)	
	Unit 22	Corymbose *Acropora* (*A. digitifera*)	YR-III core (3.2–3.1 m)	
	Unit 23	Allochthonous coral fragments (*Acropora* sp.) with associated *in situ I. palifera* and encrusting calcareous algae	YR-III core (2.8–2.3 m)	
	Unit 24	Allochthonous coral fragments (*Acropora* sp.) with associated *in situ* corals (*A. digitifera* and *I. palifera*)	YR-III core (2.0–1.6 m)	
	Unit 28	Allochthonous coral fragments (*Acropora sp.*) with associated with *I. palifera* and encrusting calcareous algae	YR-IV core (1.5–0.5 m)	

core: this patch-reef core contains five units (Units 8–12). YR-II core: this reef-crest core, composed predominantly of *in situ* corals, is divided into four bio-sedimentological units (Units 13–16). YR-V core: this reef-crest core contains five units (Units 17–21). YR-III core: this landward reef-crest core is divided into six units (Units 22–27). YR-IV core: this shallow lagoon core contains two units (Units 28 and 29).

3.2. Interpretations of facies and units

The reefs (Palau Islands and Yoron Island) are characterized by four facies (corymbose *Acropora*, arborescent *Acropora*, massive *Porites*, and detritus). These facies and their environmental conditions are listed in Table 4 and described below.

3.2.1. Corymbose Acropora facies

The corymbose *Acropora* facies, which consists of the upper part of core PL-I (Unit 4), the upper parts of cores YR-V (Units 18–21) and YR-III (Units 25–27), and core YR-II (Units 13–16), is characterized by common corals dominated by corymbose and tabular *Acropora* (*A. digitifera* and *A. hyacinthus*), robust *Acropora* (*A. robusta*/*A. abrotanoides*), and *I. palifera*. Moreover, encrusting calcareous algae and coral fragments (*Pocillopora* sp., *Montipora* sp., and *Cyphastrea* sp.) were also found in this facies. These compositions are present at the reef crest and upper reef slope in Indo-Pacific reefs. In the Ryukyu Islands, for example, these corals are found at depths of 0–7 m at Ishigaki Island (Hongo and Kayanne, 2010b; Nakamura and Nakamori, 2006) and Kikai Island (Sugihara et al., 2003). These corals are also found on distinct reef crests and upper reef slopes at other reefs (Cabioch et al., 1999; Done, 1982; Montaggioni and Faure, 1997). This zone is generally characterized by high-energy waves and low turbidity in water depths less than 7 m (Table 4).

3.2.2. Arborescent Acropora facies

The arborescent *Acropora* facies, which is limited to the lower parts of core PL-I (Units 1–3) and core PL-III (Units 8–10), is characterized by *in situ* arborescent *Acropora* (*A. muricata* and *A. intermedia*). Moreover, this facies included coral fragments (*Porites* sp., *Pocillopora* sp., and *Lobophyllia* sp.), encrusting calcareous algae, *Halimeda* fragments and calcareous sand (benthic foraminifera tests). These *in situ* corals occupy the inner reef slope and leeward reef slope at water depths of less than 20 m in the present-day Pacific Ocean (Done, 1982; Hongo and Kayanne, 2010b; Montaggioni, 2005; Nakamori, 1986). These corals are interpreted to inhabit a low- to moderate-energy environment at water depths of 0–20 m (Table 4).

3.2.3. Massive Porites facies

The massive *Porites* facies is restricted to the PL-II core (Unit 7), PL-III core (Units 11–12), and the upper section of the shallow lagoon reef in the YR-IV core (Unit 29), in which massive *Porites* is common. Based on a direct comparison with present-day reefs, this coral is interpreted to have grown in a lagoon or shallow lagoon (water depth <5 m) within a low-energy, turbid reef (Marshall and Davies, 1982; Montaggioni, 2005). Therefore, this zone is generally characterized by low-energy waves and high turbidity in water depths less than 5 m (Table 4).

3.2.4. Detritus facies

The detritus facies is limited to the lower section of the PL-II core (Units 5–6), and the YR-V (Unit 17), YR-III (Units 22–24), and YR-IV (Unit 28) cores. Allochthonous coral fragments (*Acropora* sp. and *Pocillopora* sp.), calcareous algae, gastropods, bivalves, echinoid debris, and calcareous sand (*Halimeda* fragments and benthic foraminifera tests) with associated corals (*Isopora* sp. and *Acropora* sp.) are commonly found as sediment in these sections. The depositional environment is interpreted to have been a lagoon or shallow lagoon, which is generally a low-energy setting (Montaggioni, 1988, 2005; Yamano et al., 2001).

3.3. Initiation timing of Holocene reef growth and accumulation rate

In the Palau Islands, the oldest Holocene dates (8310 cal. years BP) were obtained from the base of the arborescent *Acropora* facies at 15.1 m depth (below MSL) in core PL-I and at 24.6 m depth in core PL-III (Kayanne et al., 2002), whereas the growth of Holocene reef at Yoron Island had begun by at least 5650 cal. years BP (3.0 m deep in YR-V core). The highest accumulation rates were obtained for the arborescent *Acropora* facies, being 7.8 m/1000 years (PL-I-79 to PL-I-43) and 5.6 m/1000 years (PL-III-45 to PL-III-17). In contrast, the corymbose *Acropora* facies and massive *Porites* facies record accumulation rates of less than 3.0 m/1000 years. The corymbose *Acropora* facies records the lowest accumulation rate in the YR-V core (0.8 m/1000 years; YR-V-4 to YR-V-1) and the highest rate (2.7 m/1000 years) in the YR-II core (YR-II-3 to YR-II-1). The accumulation rates of this facies in the YR-III and PL-I cores are 1.0 m/1000 years (YR-III-2 to YR-III-1) and 1.5 m/1000 years (PL-I-43 to PL-I-3), respectively. The accumulation rate of the massive *Porites* facies in the PL-II and PL-III cores is 1.3 m/1000 years.

4. Discussion

4.1. Holocene sea-level change and reef formation

Holocene reef growth is generally influenced by some controlling factors (e.g., sea-surface temperature, sea level, wave energy, and turbidity). Sea-surface temperature (SST) is one of the most important controls on corals. The distribution is very roughly limited by the 18 °C minimum monthly isotherm because low temperature is directly related to coral physiology and survival (Sheppard et al., 2009). For Great Barrier Reef corals, all metabolic activities (including photosynthesis and calcification) progress at an optimal rate at a temperature of around 27 °C, and if the temperature is higher than that, the rate of these metabolic activities is accelerated in an increasingly uncontrolled way (Veron, 2008). The present-day SST ranges from 28 to 30 °C in Palau Islands (Morimoto et al., 2002) and from 21 to 28 °C in Yoron Islands (Japan Meteorological Agency; see http://www.data.kishou.go.jp/kaiyou/db/kaikyo/dbindex.html); consequently, the study area is one of the most optimum sites for reef growth.

The Palau Islands are located within the Indo-Pacific Warm Pool (IPWP). A comparison of reconstructed Holocene SST with present-day values in the IPWP region, based on foraminifera Mg/Ca values, alkenone, and coral Sr/Ca thermometry, reveals no significant differences between the two periods (Gagan et al., 2004; Stott et al., 2004). In the Ryukyu Islands, there is little difference between the estimated Holocene SST and the present-day SST, although the record of the abundance of planktonic foraminifera (*Pulleniatina obliquiloculata*) indicates a cooling event at 4600–2700 years BP (Jian et al., 2000). The estimated Holocene SST at the southern Ryukyu Islands (25°12′N, 123°07′E) was 21.5–26.6 °C for winter and 28.2–29.1 °C for summer; the present-day values are 23.2 °C for winter and 29.1 °C for summer (Jian et al., 2000). In the northern Ryukyu Islands (31°29′N, 128°31′E), the Holocene SST was 18.4–26.0 °C for winter and 27.2–28.9 °C for summer; the present-day values are 18.5 °C for winter and 28.5 °C for summer (Jian et al., 2000). Moreover, the results of numerical experiments indicate no change in SST in this region during the Holocene (Kutzbach et al., 1998). Therefore, this finding indicated that SST is important for the existence of corals during the Holocene, but that it is probably unimportant for temporal and spatial changes of coral during this period.

Holocene sea-level change is another important controlling factor for reef growths. A change in accommodation space is thought to be a driver of reef growth. Kennedy and Woodroffe (2002) proposed that accommodation space controlled by sea level position has exerted an influence on environmental changes (e.g., water depth, wave energy, and sediment input) during the Holocene. For example, Montaggioni and Faure (1997) showed that changes in coral community and reef growth in Mauritius reef from Indian Ocean were driven principally by increasing water energy due to the decrease in accommodation space. Macintyre (2007) determined that reef growth history in the Caribbean was controlled by a change in accommodation space and water energy, and response to the sea-level change during the Holocene. These scenarios are also observed at other reefs (e.g.,

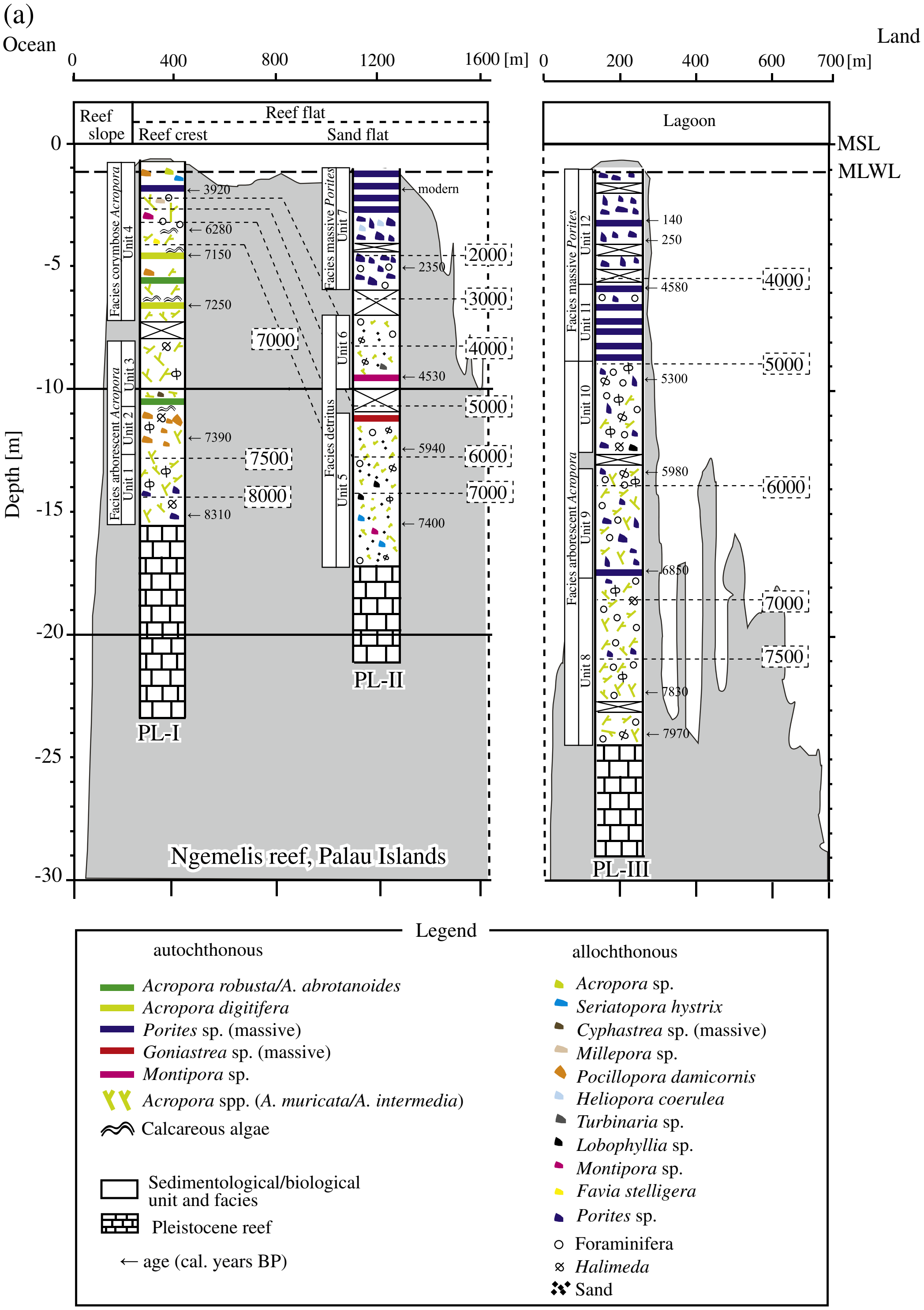

Fig. 2. Topographic profiles and internal structure of Holocene coral reef at (a) Ngemelis reef in the Palau Islands and (b) Kurohana reef at Yoron Island. Cross-section with interpolated time–growth lines showing the sedimentological characteristics of drilling cores and 29 calibrated radiocarbon ages. Twenty-eight sedimentological units (Units 1–28) and 4 main facies (facies corymbose *Acropora*, facies arborescent *Acropora*, facies massive *Porites*, and facies detritus) are observed from the study sites. Main characteristics and distribution of sedimentary units, and distribution and paleoenvironmental interpretation of facies are described in Table 4. MSL and MLWL indicate mean sea level and mean lowest water level, respectively.

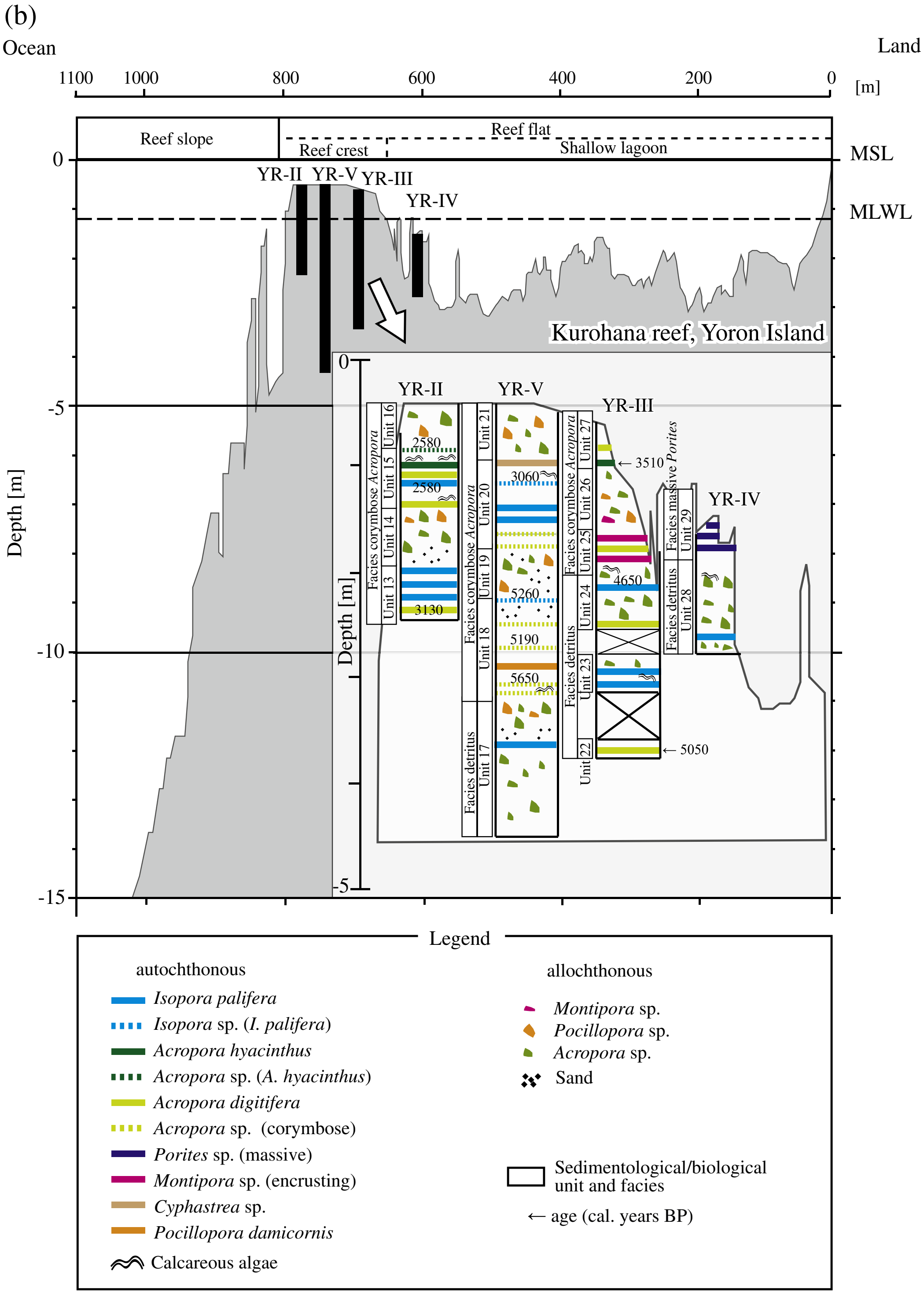

Fig. 2 (*continued*).

Cabioch et al., 1995; Davies et al., 1985; Grossman and Fletcher, 2004; Hubbard et al., 2005). Therefore, Holocene sea-level change plays major roles in determining the sedimentary facies and corals on reefs from the Caribbean and Indo-Pacific regions.

Sea-level curves constructed for the northwest Pacific (Hongo and Kayanne, 2010a; Ota et al., 2000; Yokoyama et al., 1996) indicate that flooding of the antecedent substrate at the Palau Islands occurred at 9000–8200 cal. years BP (Fig. 3). The timing of initial reef growth at Yoron Island remains unknown because the base of the Holocene reef was not recovered in cores; however, reef formation at the Palau Islands began within 1000 years of inundation of the substrate, indicating initial reef growth during the period 8310–7970 cal. years BP. Although some reefs initiated from 23,000 to 10,000 years ago (e.g., Vanuatu: Cabioch et al., 2003; Tahiti: Montaggioni et al., 1997; Huon Peninsula in Papua New Guinea: Chappell and Polach, 1991), reefs in the Indo-Pacific region generally began growing at 10,000–7000 cal. years BP (e.g., Cabioch et al., 1995; Camoin et al., 1997, 2004; Davies et al., 1985; Kan and Kawana, 2006; Kan et al., 1995).The timing of initial reef growth at the Palau Islands is consistent with that at other sites. The obtained sea-level curves show a rapid rise between

Table 5
Coral species list in the cores of Palau Islands and Yoron Island.

Family Pocilloporidae	
Seriatopora	*Seriatopora hystrix* *Seriatopora* sp.
Pocillopora	*Pocillopora damicornis* *Pocillopora meandrina*? *Pocillopora* sp.
Family Acroporidae	
Acropora	*Acropora abrotanoides* *Acropora digitifera* *Acropora hyacinthus* *Acropora intermedia* *Acropora muricata* *Acropora robusta* *Acropora* sp.
Montipora	*Montipora* sp.
Isopora	*Isopora palifera*
Family Poritidae	
Porites	*Porites* sp.
Family Mussidae	
Lobophyllia	*Lobophyllia* sp.
Family Faviidae	
Goniastrea	*Goniastrea sp.*
Cyphastrea	*Cyphastrea* sp.
Favia	*Favia stelligera*
Family Dendrophyllidae	
Turbinaria	*Turbinaria fromdens*?
Family Helioporidae	
Heliopora	*Heliopora coerulea*
Family Milleporidae	
Millepora	*Millepora* sp.

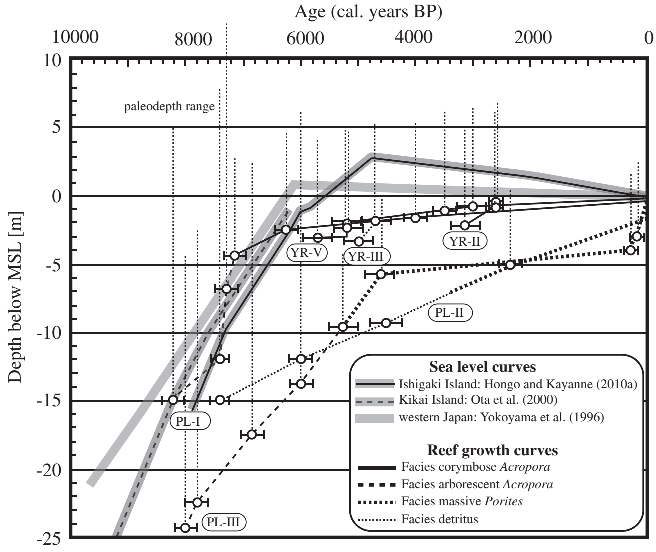

Fig. 3. Reef growth and sea-level curves for the Palau Islands and Yoron Islands. Reef growth curves in this study are shown by a combination of solid line, dashed line, and dotted line. Solid line and dashed line indicate facies corymbose *Acropora* and facies massive *Porites*, respectively. Thick and thin dotted lines show facies arborescent *Acropora* and facies detritus, respectively. Radiometric counter errors for ^{14}C dates are given by 2 σ. Each plot is positioned with respect to present mean sea level. The vertical bar above each plot represents the paleowater depth range based on environmental conditions. Sea-level curves for the western Pacific proposed by Hongo and Kayanne (2010a), Ota et al. (2000) and Yokoyama et al. (1996), are shown by shaded lines.

9000 and 6000 cal. years BP, following by stabilization (Fig. 3). In the Palau Islands, upward reef growth began soon after the sea-level rise, although the rate of reef growth decreased once the sea level had stabilized. The change in growth rate is interpreted to reflect a decrease in the accommodation space available for upward growth. At Yoron Island, the change in growth rate that followed the stabilization of sea level is consistent with that recorded at the Palau Islands (Fig. 3). The patterns of reef accretion at Okinoerabu Island (Kan et al., 1995) and Ishigaki Island (Hongo and Kayanne, 2009) are also consistent with this growth mode. These growth styles are also observed at New Caledonia (Cabioch et al., 1995), Mauritius (Camoin et al., 1997), and Mayotte (Camoin et al., 1997), and consequently the reef growth pattern at the Palau Islands and Yoron Island is consistent with that at other sites.

4.2. Key species for reef formation during the Holocene

Arborescent *Acropora* (*A. muricata* and *A. intermedia*) was a dominant reef builder in the lower parts of Holocene reef crests and patch reefs (arborescent *Acropora* facies) in the Palau Islands during Holocene sea-level rise (Figs. 3, 4). In the reef crest, the reef was piled up with arborescent *Acropora* until around 7300 cal. years BP. During the stage of rapid upward growth (7.8 m/1000 years), the ocean environment was a low- to moderate-energy setting in which the reef grew under conditions of increasing accommodation space and was protected from seasonal winds and swells. Consequently, the corals in the reef crest were reef builders, even though the reef faced the open ocean. The coral community in the patch reef also consisted of reef builders because the environment of the patch reef upon the lagoon was generally a low- to moderate-energy setting. The formation of this patch reef continued for approximately 2700 years (7970–5300 cal. years BP). Although the species of this reef remain unknown, a patch reef at Sekisei reef (Ryukyu Islands) records the rapid accumulation (9.3 m/1000 years) of arborescent *Acropora* during the period of Holocene sea-level rise (Kan and Kawana, 2006). Therefore, arborescent *Acropora* (*A. muricata* and *A. intermedia*) were the key species for reef formation under low- to moderate-energy conditions during the period of sea-level rise.

Corymbose and tabular *Acropora* (*A. digitifera*) and robust *Acropora* (*A. robusta*/*A. abrotanoides*) are the dominant reef builders above the arborescent *Acropora* facies in the Palau Islands (Figs. 3, 4). Vertical reef growth started at ~7300 cal. years BP, from when the growth rate decreased from 7.8 to 1.5 m/1000 years. This trend is explained by the specific response to the build-up to environmental conditions, resulting in the replacement of arborescent *Acropora* by corymbose and robust *Acropora*, which are better adapted to changes in accommodation space and the energy level of the growth environment, because the corymbose, tabular, and robust *Acropora* were restricted to a shallow-water environment (<7 m depth) following sea-level stabilization. Moreover, during the period following the stabilization of sea level, the upper part of the reef crest at Yoron Island consisted predominantly of corymbose and tabular *Acropora* (*A. digitifera* and *A. hyacinthus*) and *I. palifera* (Figs. 3, 4). During this period, the environment was characterized by high-energy conditions, indicating that corymbose, tabular, and robust *Acropora* (*A. digitifera*, *A. hyacinthus*, and *A. robusta*/*A. abrotanoides*) and *I.palifera* were the main reef builders under high-energy conditions once sea-level had stabilized. The coral community also played an important role in reef growth during the period of sea-level rise. For example, the windward reef (Ibaruma reef) at Ishigaki Island consisted mainly of *A. digitifera* and *A. hyacinthus* during the period of sea-level rise (Hongo and Kayanne, 2009); consequently, these corals were the main reef builders under high-energy conditions during the period of Holocene sea-level rise and stabilization.

Massive *Porites* was also one of the reef builders, although only during the stage of sea-level stabilization (Fig. 3). In the Palau Islands, coral was observed in the upper parts of the patch reef and reef flat. Vertical reef growth by the coral started at ~5300 cal. years BP above the arborescent *Acropora* facies in the patch reef and at ~2400 cal. years BP above the detritus facies upon the reef flat. The zone behind the reef crest was a lagoon or shallow lagoon, representing low-energy, turbid conditions. The same finding was also obtained for Yoron Island. Massive *Porites* grew above the detritus facies in the shallow lagoon (Figs. 3, 4). Furthermore, massive *Porites* was a significant reef builder at Ishigaki Island in the shallow lagoon under low-energy, turbid conditions after sea level had stabilized (Hongo and Kayanne, 2010b). Kan and Kawana (2006) reported that massive *Porites* appeared in the area lagoonward of the reef crest after sea level had stabilized (4160 cal. years BP). Although the identification of massive *Porites* (*Porites* sp.) is restricted to the genus level, this coral was the key species under low-energy, turbid conditions during the period after sea level had stabilized.

During the period of Holocene sea-level rise and stabilization, corymbose, tabular, and arborescent *Acropora*, *I. palifera*, and *Porites* were the main key species for reef growth in the Indo-Pacific (e.g., Cabioch et al., 1995, 2003; Camoin et al., 1997, 2004; Cortés et al., 1994; Grossman and Fletcher, 2004; Kan and Hori, 1993; Kan and Kawana, 2006; Konishi et al., 1978; Marshall and Davies, 1982; Montaggioni and Faure, 1997; Ota et al., 2000; Takahashi et al., 1988; Webster et al., 1998; Yamano et al., 2001, 2003;). Although previous works have been restricted to genus-level taxonomical identification, Ota et al. (2000) reported that the Holocene reef at Kikai Island consisted of *A. digitifera*, *A. hyacinthus*, *A. gemmifera*, and *I. palifera* during the past 6000 years. Moreover, Webster et al. (1998) indicated that *A. hyacinthus*, *A. monticulosa*, and *I. palifera* were the main reef builders in the Holocene reef at Kikai Island. Holocene reef at Mayotte was represented by a single facies dominated by robust *Acropora* (*A. robusta*/*A. abrotanoides*) and the environment was characterized by high-energy conditions and increasing sea level (Camoin et al., 2004). In Oahu Island from Hawaii, Holocene reef comprised mainly *Porites compressa* and *Porites lobata* (Grossman and Fletcher, 2004). These data support that these corals (*A. digitifera*, *A. hyacinthus*, *A. robusta*/*A. abrotanoides*, *A. muricata*, *A. intermedia*, *I. palifera*, and *Porites*) were key species for Holocene reef formation in the Indo-Pacific region.

Key species in the Caribbean reefs are different from those of the Indo-Pacific region. Two *Acropora* species (*A. palmata* and *A. cervicornis*) are main reef builders in the Caribbean (e.g., Aronson et al., 2005; Blanchon et al., 2002; Gischler and Hudson, 2004; Hubbard et al., 2005) and these species are characterized by endemic species in this region. However, the growth form of *A. palmata* and *A. cervicornis* is characterized by robust and arborescent, indicating that these species are similar to key species in the Indo-Pacific in their forms. This finding indicates that there is a principle for reef formation during sea-level changes.

Drowned reefs between the Last Glacial Maximum (LGM) to 10,000 years ago would be composed of different key species. These drowned reefs were observed from Vanuatu (Cabioch et al., 2003), Marquesas (Cabioch et al., 2008), Great Barrier Reef (Beaman et al., 2008), Ryukyu Islands (Sasaki et al., 2006), the Indian Ocean (Dullo et al., 1998), and the Caribbean (Fairbanks, 1989). Although little is known about species-level identification of corals, for example, Vanuatu reef from 23,000 to 11,500 years ago was characterized by tabular and branching *Acropora* in medium to high-energy conditions (Cabioch et al., 2003). In Irabu Island, Ryukyu Islands from 25,000 to 13,000 years ago consisted of *Favia pallida*, *Favia* sp., *Platygyra* sp., *Cyphastrea* sp., *Plesiastrea versipora*, *Stylocoeniella* sp., and *Seriatipora* sp. (Sasaki et al., 2006). These corals are characterized by the upper part of the reef slope, from 5 to 20 m in water depth, in the Ryukyu Islands (Nakamori, 1986). This finding indicates that reef builders between LGM to around 10,000 years ago may mainly reflect the rapid sea-level change (Bard et al., 1996, 2010; Chappell and Polach, 1991; Fairbanks, 1989). Moreover, a difference in the key species for reef formation since the last deglaciation was interpreted as other environmental factors (e.g., substrate, nutrient level, terrigenous input, and sea-surface temperature). Montaggioni (2005) recognized these factors are generally important to influence reef growth, but it is necessary to gain more data from drowned reefs.

4.3. Ecological strategies of key species

Key species for Holocene reef formation is mainly *Acropora*, which is commonly regarded as a genus of evolutionarily successful corals because of the following three skeletal characteristics: small corallites for fine detail in skeletal development, a division of axial and radial corallites for highly deterministic growth forms, and porous skeletal microstructures for maximum strength relative to weight (Veron, 1995). These characteristics enable rapid growth, determinate growth, a high degree of colony integration, and rapid local dispersion via fragmentation (Veron, 1995). Moreover, corymbose, tabular, and robust forms of key species (*A. digitifera*, *A. hyacinthus*, and *A. robusta*/*A. abrotanoides* in the Indo-Pacific and *A. palmata* in the Caribbean) have highly integrated skeletal characteristics, making them well suited to rapid exploitation and continuous growth. Their preferred habitat (high-energy conditions, good light penetration, and high oxygen concentrations) enables vigorous upward growth, and these growth forms are strongly resistant to wave action, which is advantageous for reef growth. Arborescent key species (*A. muricata* and *A. intermedia* in the Indo-Pacific and *A. cervicornis* in the Caribbean) also contributed to rapid exploitation and continuous growth, although restricted to low- to moderate-energy conditions because the key species were generally characterized by a fragile structure and rapid growth rate in excess of 150 mm/years (Gomez et al., 1985). It is possible that these features are the important principle of key species and consequently key species have the advantage of rapid vertical reef growth during periods of marked environmental change, such as Holocene sea-level change.

Moreover, the initiation of coral settlement with regard to key species is important for reef formation. The colonization of new reefs by corals is generally accomplished by planula larvae, which drift within ocean currents to new locations where they settle and grow. The effectiveness of transportation of coral can be attributed to oceanographical and biological factors such as ocean currents, length of larval life, stepping stones, rafting, and El Niño–Southern Oscillation (ENSO) influences (e.g., Glynn and Ault, 2000; Grigg and Hey, 1992; Harii et al., 2010; Jokiel, 1984). For example, coral larvae capable of long distance dispersal have been found at various distances across the east Pacific (Glynn and Ault, 2000). Jokiel (1984) described that geographic dispersal of corals by rafting of mature colonies provides an attractive alternative to larval dispersal because it allows for a much longer drift time. Some Indo-Pacific species have been transported into the east Pacific during the 1997–1998 ENSO event because ENSO events are characterized by sudden and marked changes in circulation routes and transport rates can greatly influence west-to-east dispersal pathways (Glynn and Ault, 2000).

The majority of key species identified above are spawners, releasing sperm and eggs into the water (Richmond and Hunter, 1990). Spawning may occur only once a year, several days following the summer full moon (Harrison et al., 1984). The resulting planulae lack zooxanthellae and appear to have a shorter competence period than brooded *Pocillopora* larvae (Harrison et al., 1984), however, *A. digitifera* has an observed competence period of at least 54 days (Nishikawa and Sakai, 2005). Moreover, the larvae of corymbose *Acropora* (*A. tenuis*) have a competence period of 20–69 days (Nishikawa et al., 2003; Richmond, 1988). Consequently, these results indicate that coral larvae generally settle within 1–2 months of release.

In the northwest Pacific, this area is characterized by archipelagos from the Solomon Islands to the Ryukyu Islands. The distribution of these islands creates stepping stones to bridge the gap between adjacent islands which are in the range of tens to hundreds of kilometers. In this region, the western boundary current (Kuroshio) flows along these islands with a typical present-day surface current of 0.3–2 m/s (Maximenko et al., 2009; Open University, 2001). The ENSO influences the interannual variability of the Kuroshio Current, although seasonal variations are greater than interannual variations (Qu et al., 2004). The reconstructed paleoclimate record indicates fluctuations in the Kuroshio Current during the Holocene (Sun et al.,

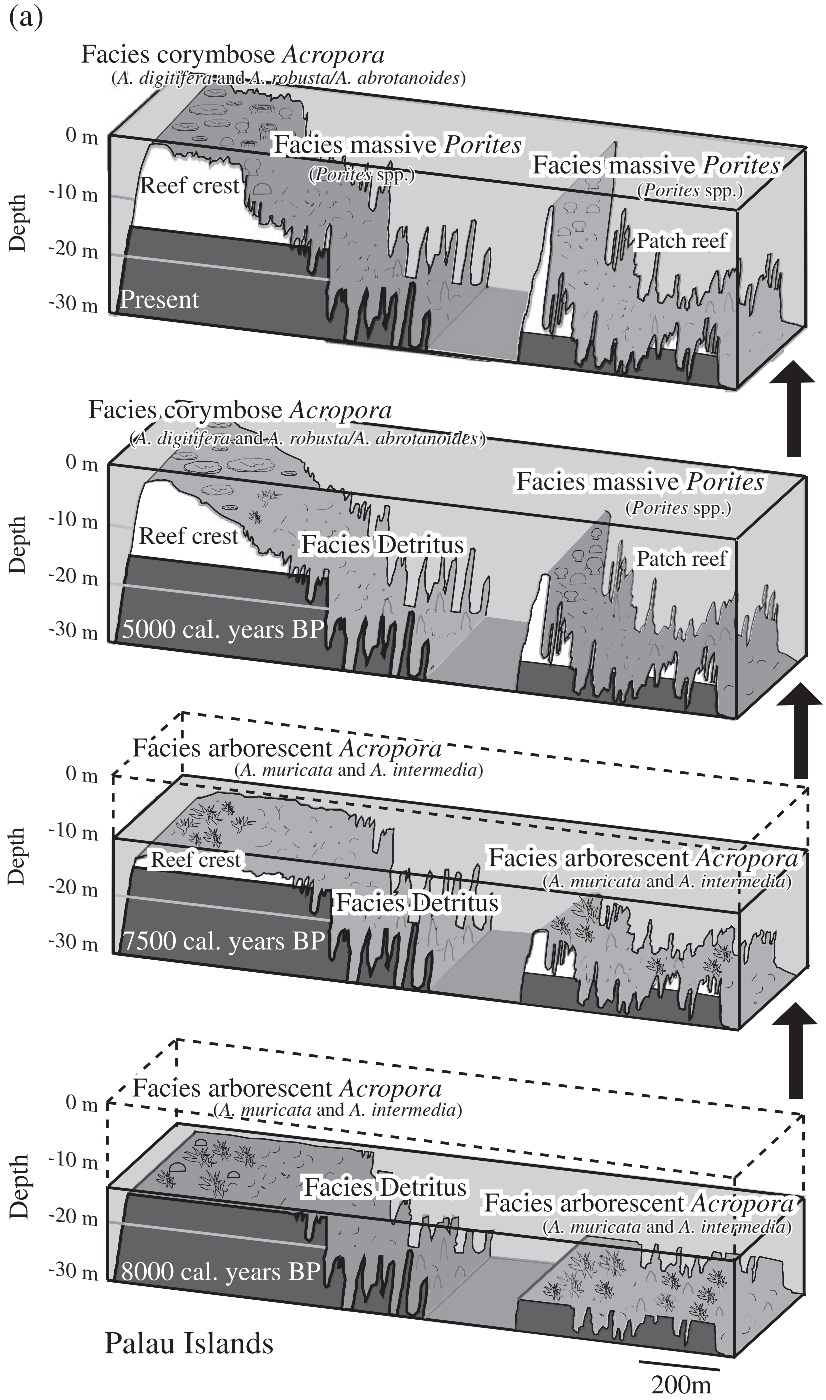

Fig. 4. Holocene reef history on (a) the Palau Islands and (b) Yoron Island, showing the temporal and spatial distributions of key species and facies. (a) In the Palau Islands, the earliest reefs date to around 8000 cal. years BP and the reef crest and the patch reef in lagoon were dominated by facies arborescent *Acropora* (*A. muricata* and *A. intermedia*). Reef flat was dominated by facies detritus. After 8000 cal. years BP, the reef continued to build, but the reef crest and the patch reefs were dominated by facies corymbose *Acropora* (*A. digitifera* and *A. robusta*/*A. abrotanoides*) and facies massive *Porites* (*Porites* spp.) at 5000 cal. years BP respectively, probably a response to changes in wave energy level and decreases in accommodation space of the growth. After 5000 cal. years BP, the reefs were characterized by upward and lateral growth, and the reef flat was dominated by facies massive *Porites* (*Porites* spp.), interpreted as a response to changes in environmental condition. At present, the reefs have reached sea level, and are dominated by facies corymbose *Acropora*, facies massive *Porites*, and facies arborescent *Acropora*. (b) In Yoron Island, the initiation timing is unknown, but the reef growth started before 5000 cal. years BP. The reef crest and shallow lagoon comprised facies corymbose *Acropora* (*A. digitifera*, *A. hyacinthus*, *A. robusta*/*A. abrotanoides*, and *I. palifera*) and facies detritus, respectively. After 5000 cal. years BP, the reef crest and the shallow lagoon continued to pile up, but the latter was dominated by facies massive *Porites* (*Porites* spp.), probably in response to changes in environmental conditions (e.g., turbidity and wave energy). Presently, the reefs are dominated by facies corymbose *Acropora* and facies massive *Porites*.

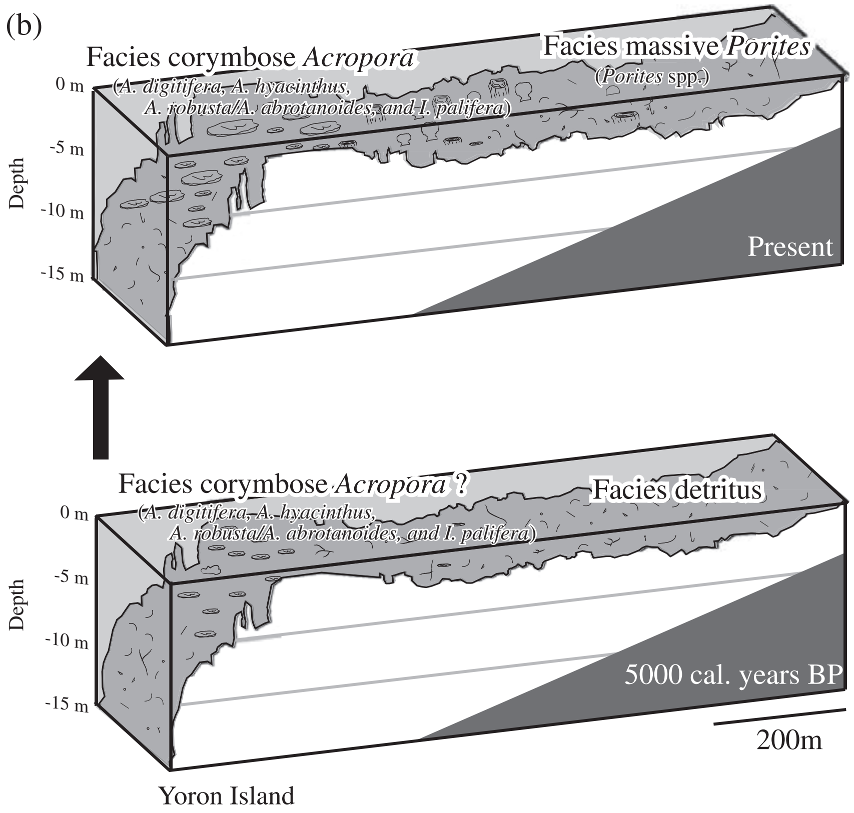

Fig. 4 (*continued*).

2005; Xiang et al., 2007). Although the velocity of the Kushiro during the Holocene remains unknown, the northwest Pacific is assumed to have been dominated by a continuous northward current. Consequently, assuming that coral larvae remain in the water column after release, the dispersal distance would have been more than 700 km. Therefore, it is relatively easy for the key species to distribute and contribute reef formation throughout the northwest Pacific during the period of Holocene sea-level rise and stabilization.

4.4. Present-day decline in coral reefs and restoration plans

Corals currently face a worldwide mortality, and mass-bleaching events are thought to have a greater effect on key species than on other species (Aronson et al., 2004, 2005; Fujioka, 1999; Gardner et al., 2003; Sugihara et al., 1999). For example, Fujioka (1999) reported that *A. hyacinthus* was completely bleached (100%) at Ishigaki Island during the 1998 bleaching event, whereas the overall mortality due to bleaching was 60.7%. Corymbose and tabular *A. digitifera* and *A. hyacintus*, which represent the main reef builders on the reef crest at Ishigaki Island, were almost completely wiped out during the 2007 bleaching event. In the reef crest at the Palau Islands after the 1998 bleaching event, the previously dominant *A. digitifera* was replaced by massive *Porites* and the amount of living coral cover decreased from 8.1 to 1.4% (Golbuu et al., 2007; Kayanne, 2007). High SSTs have caused severe bleaching of coral worldwide, and such events have become more frequent at coral reefs worldwide over the past two decades (Glynn, 1993; Hoegh-Guldberg, 1999). Moreover, in the case that SSTs rise by 2–3 °C, annual bleaching is expected to become commonplace throughout the world (e.g., Wilkinson and Souter, 2008).

To restore coral reefs, the transplantation of coral fragments has been considered a useful technique since the 1980s. Fragments of tabular *A. hyacinthus* showed a 100% survival rate after 14 months, indicating that this species is well suited to transplantation (Okubo et al., 2005). However, most previous experiments on coral transplantation have been restricted to arborescent *Acropora* such as *A. muricata* and *A. intermedia* because such corals are characterized by a high growth rate (Lindahl, 2003; Okubo and Omori, 2001; Soong and Chen, 2003). The present results indicate that *A. robusta*/*A. abrotanoides* and *I. palifera* are among the main reef builders on high-energy reefs; consequently, further studies are required regarding the transplantation of these key species to ensure the long-term sustainability of reef ecosystems.

Changes in the spatial and temporal scales of connectivity have implications for the management of coral reef ecosystems, especially the design and placement of MPAs (Munday et al., 2009). Therefore, the present findings regarding the relationship between reef formation and key species during the Holocene indicate that the size and location of protected areas must be determined based on fundamental geological evidence regarding the key species.

5. Conclusions

The present analysis of Holocene cores recovered from the Palau Islands and Yoron Island provide species-level records for periods of reef growth, leading to the following conclusions.

(1) At the Palau Islands, 12 biological and sedimentological units (Units 1–12) were identified from three cores, whereas at the Yoron Islands, 17 units were identified (Units 13–29). Based on the occurrence of common corals and sediment among these units, four major facies were identified in the study sites. The corymbose *Acropora* facies is restricted to the upper part of the PL-I core (Unit 4), the upper parts of the YR-V (Units 18–21) and YR-III cores (Units 25–27), and the YR-II core (Units 13–16), and is dominated by corymbose and tabular *Acropora* (*A. digitifera* and *A. hyacinthus*) and *I. palifera*. The arborescent *Acropora* facies, which occurs in the lower parts of the PL-I (Units 1–3) and PL-III cores (Units 8–10), is dominated by *in situ* arborescent *Acropora* (*A. muricata* and *A. intermedia*). The massive *Porites* facies, which

is restricted to the PL-II (Unit 7) and PL-III cores (Units 11–12), and the upper part of the shallow lagoon reef in the YR-IV core (Unit 29), is dominated by massive *Porites*. Finally, the detritus facies, which occurs in the lower parts of the PL-II (Units 5–6), YR-V (Unit 17), YR-III (Units 22–24), and YR-IV cores (Unit 28), is dominated by allochthonous coral fragments and calcareous sand.

(2) The occurrence of Holocene reefs coincided with a sea-level rise, followed by stabilization. Arborescent *Acropora* (*A. muricata* and *A. intermedia*) was a key species for reef formation under low- to moderate-energy conditions during the period of sea-level rise. Corymbose, tabular, and robust *Acropora* (*A. digitifera*, *A. hyacinthus*, and *A. robusta*/*A. abrotanoides*), as well as *I. palifera*, were the main reef builders under high-energy conditions during the period of Holocene sea-level rise and stabilization. Massive *Porites* was a key species under low-energy, turbid conditions (lagoon or shallow lagoon setting) once sea level had stabilized.

(3) Key species in the Indo-Pacific and the Caribbean are characterized by common skeletal characters, which enable rapid growth, determinate growth, a high degree of colony integration, strongly resistant to wave action, and rapid local dispersion via fragmentation. These features are a principle for reef formation during sea-level changes.

(4) The skeletal characteristics of the key species enabled vigorous reef formation during the period of Holocene sea-level change; however, these species are currently more strongly affected by mass-bleaching events than are other species. Therefore, further studies are required concerning transplantation and the appropriate size and location of MPAs based on the geological record of key species, to ensure the long-term health of modern-day coral reefs.

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