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Biogeography of Holocene coral species in the western Indian Ocean

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ABSTRACT

Understanding the relationship between coral biogeography and reef development is a key topic in sedimentology and paleoecology. Although the knowledge of coral reef growth and internal facies patterns during the Holocene has increased since the 1970s, the biogeography of Holocene coral species in the Indo-Pacific regions remains poorly constrained. In this study, we examined quantitative records of coral species based on data from five cores retrieved from two Holocene reefs in the western Indian Ocean: La Pointe-au-Sable reef on Mauritius Island and Toliara reef on Madagascar. Our results indicate that the dominant reef-building corals on both reefs were *Isopora palifera*, *Acropora robusta*/*abrotanoides* complex. Some corals (e.g., the *A. robusta*/*abrotanoides* complex and *Acropora digitifera*) from 6 ka were found in Mauritius, whereas these were not identified in the cores from Madagascar before 1.5–1 ka. This delay may have been controlled by ocean currents and/or the competency period of the coral larvae. A comparison of these coral assemblages with those in other regions (Seychelles, Mayotte, Ryukyu Islands, Palau Islands, Papua New Guinea, the Great Barrier Reef, New Caledonia, and Vanuatu) showed that *I. palifera* was common in all of the studied regions, whereas *Goniastrea retiformis* probably migrated recently to Mauritius and Madagascar in response to prevailing surface ocean currents, including the South Equatorial Current and the Agulhas Current. One explanation for the late arrival of *G. retiformis* to the study sites could be that the competency period of *G. retiformis* larvae is shorter than that of *I. palifera*. Moreover, our quantitative analysis suggests that a given population size during the Holocene may have contributed to the abundance of species in modern reefs. This study emphasizes the need for further quantitative research on Holocene coral species in other regions to better understand the temporal and spatial patterns of coral biogeography.

1. Introduction

The origin, distribution, and diversity of reef-building coral species are controlled by physical factors (e.g., sea surface temperature (SST), salinity, light intensity, hydrodynamic factors, ocean circulation, and sediment input), biological factors (e.g., spawning mode and competency period), and geological factors (plate tectonics, substrate availability, closure and opening of seaways, global cooling and warming events, and sea-level fluctuations) (Grigg and Hey, 1992; Pandolfi, 1992; Veron, 1995). At present, the numbers and abundances of coral species recorded in Indo-Pacific provinces are spatially variable. For example, over 200 coral species have been recorded in the Indian Ocean (Veron, 1995), whereas up to 350 species have been recorded around Australia (Spalding et al., 2001). The dominant species also vary among the regions (e.g., the western Indian Ocean, the northwest Pacific, and the southwest Pacific), although the major reefal environmental conditions are reasonably similar throughout the tropical zone. At present in the western Indian Ocean, *Acropora digitifera*, *Acropora humilis*, and *Acropora abrotanoides*, all with wave-resistant growth forms, dominate the coral assemblages in the reef crest zone of Mauritius (Montaggioni and Faure, 1997). In the northwest Pacific, *A. digitifera*, *Acropora hyacinthus*, and *Goniastrea retiformis* are currently the dominant forms in the same zone in Ishigaki Island in the Ryukyu Islands (Hongo and Kayanne, 2010), whereas *A. humilis*, *A. digitifera*, and *A. hyacinthus* are prominent taxa on the Ngemelis barrier reef in the Palau Islands (Kayanne et al., 2002). In the southwest Pacific, *A. humilis* and *Isopora palifera* are prominent taxa in the reef-crest zone in the central Great Barrier Reef (Done, 1982). On Huon Peninsula, Papua New Guinea, *A. hyacinthus*, *A. humilis*, *Acropora monticulosa*, and *Acropora robusta* are dominant species (Nakamori et al., 1995a). In New Caledonia, *A. digitifera*, *A. humilis*, *A. abrotanoides*, *A. robusta*, *Acropora milleopora*, *Acropora valida*, and *Pocillopora verrucosa* are dominant species on the Ricaudy Reef (Cabioch et al., 1999). One explanation for the local differences in the composition of coral species is the pattern of gene flow, demonstrated with molecular data (e.g., allozymes and mitochondrial DNA).

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These show that the distribution of coral reef species across the Indo-Pacific regions does not reflect the modern ocean circulation regimes (Benzie, 1999). Therefore, the present patterns of genetic variation in the Indo-Pacific may have resulted from highly pulsed dispersal events associated with coral range expansions during interglacial periods. Moreover, during the last glacial maximum (LGM), coral reefs in the Indo-Pacific region were isolated by barriers that emerged during low sea-level stands, such that corals in the Red Sea, Madagascar, Maldives, and southwest Asia–Australia regions were isolated from one another (Benzie, 1999; Pellissier et al., 2014). Thus, most coral species survived the last glacial period in isolated refuges (Veron, 1995), and the pool of modern coral species in a given region would have been repopulated from these pre-existing refuges during deglacial sea-level rise (Veron, 1995). However, stages of reef-building and the temporal and spatial patterns of coral species in Indo-Pacific regions during the last deglaciation are still largely unknown.

Quantitative data on the temporal and spatial patterns of fossil coral species in Indo-Pacific regions are probably essential if we are to identify the factors that control the abundance of corals on modern reefs. These data relate to the percentage abundances of the corals, derived from paleontological and/or ecological methods (e.g., quadrat and/or belt transects, binary presence/absence data). A small coral population probably means that the population has been isolated. Such an isolation may cause a reduction in genetic diversity from genetic drift. This implies that the relevant coral species are likely to have a limited capacity to respond to environmental change (Ayre and Hughes, 2004). It also implies that the long-term dominant species at a given reef site probably contribute to the dominant species on the modern reef, although a variety of environmental factors can change, affecting the composition of the coral population.

Although coral samples extracted from reef coring have been identified at the species level, most previous studies have been limited to qualitative analyses of coral assemblage compositions, with the aim of reconstructing the history of Holocene reef development in relation to environmental changes (e.g., Montaggioni, 2005; Bard et al., 2010; Roff et al., 2013). The most detailed descriptions of reef development come from regions with low species diversity, such as the Caribbean, or from exposed but well-preserved reefal outcrops in tectonically active areas, such as in Papua New Guinea and the Ryukyu Islands (Table 1). For example, Nakamori et al. (1995b) reported that the Holocene reef terraces at Kanzaura and Kwambu in Papua New Guinea are dominated by *A. humilis*, *I. palifera*, *A. hyacinthus*, and *A. monticulosa*. At Kikai Island in the Ryukyu Islands, Holocene reefs are predominantly composed of tabular and massive corals (*A. humilis*, *A. hyacinthus*, *A. monticulosa*, *I. palifera*, *Leptoria phrygia*, *Porites australiensis*, *Porites lutea*, *Porites lobata*, and *P. verrucosa*) (Webster et al., 1998; Sugihara et al, 2003). Only a few studies have focused on the time spanning the last deglaciation (for instance, Tahiti: Montaggioni et al., 1997; Abbey et al., 2011; the Great Barrier Reef: Webster and Davies, 2003; Papua New Guinea: Nakamori et al., 1995b; Pandolfi et al., 2006; Palau Islands: Hongo and Kayanne, 2011; New Caledonia: Hongo and Wirrmann, 2015; Mayotte: Camoin et al., 1997, 2004; Seychelles: Camoin et al., 2004; Mauritius: Montaggioni and Faure, 1997). At Ribbon Reef 5 and Boulder Reef on the Great Barrier Reef, the *A. robusta/abrotanoides* complex, *A. humilis/monticulosa* complex, *I. palifera*, *Stylophora pistillata*, and *P. verrucosa* are the main contributors to Holocene reef formation (Webster and Davies, 2003). In the Ryukyu Islands, *Astrea curta*, *A. digitifera*, *A. hyacinthus*, and *Dipsastraea stelligera*, have been the dominant species in reef-crest formation on Ishigaki Island since 7.8 ka (1 ka = 1000 years ago) (Hongo and Kayanne, 2009). *Acropora digitifera*, the *A. robusta/abrotanoides* complex, and the *Acropora muricata/intermedia* complex have been the dominant reef-crest builders on the Palau Islands since 8.3 ka (Hongo and Kayanne, 2011). At Mayotte, the *A. robusta/abrotanoides* complex and *G. retiformis* have been the dominant reef builders since 9.6 ka (Camoin et al., 1997, 2004). In the Seychelles, the *A. robusta/abrotanoides* complex, *G. retiformis*, *P. verrucosa*, *Galaxea fascicularis*, *L. phrygia*, and *S. pistillata*

Table 1
Survey of quantitative and qualitative assessments of Holocene coral species conducted in different studies.

Reef location	Area	Region	Sampling method	Sampling quality	Cited reference
Galeta reef	Panama	Caribbean	Drilled core	qualitative	Macintyre and Glynn (1976)
Channel Cay	Belieze	Caribbean	Submarine trench and drilled core	quantitative[†]	Aronson and Precht (1997)
Channel Cay and other cays	Belieze	Caribbean	Drilled core	quantitative[†]	Aronson et al. (2002)
Pamandzi reef	Mayotte	Western Indian Ocean	Drilled core	qualitative	Camoin et al. (1997, 2004)
Anse aux Pins reef	Seychelles	Western Indian Ocean	Drilled core	qualitative	Camoin et al. (2004)
La Pointe-au-Sable reef	Mauritius	Western Indian Ocean	Drilled core	qualitative	Montaggioni and Faure (1997)
Reefs at Pacific coast	Panama	NE Pacific	Drilled core	qualitative	Glynn and Macintyre (1977)
Punta Islotes reef	Golfo Dulce, Costa Rica	NE Pacific	Drilled core	qualitative	Cortés et al. (1994)
Kaneohe Bay and Hilo Bay	Oahu Island, Hawaii Islands	NE Pacific	Drilled core	qualitative	Grigg (1998)
Kailua Bay	Ohau Island, Hawaii Islands	NE Pacific	Drilled core	qualitative	Grossman and Fletcher (2004)
Ibaruma reef	Ishigaki Island, Ryukyu Islands	NW Pacific	Drilled core	qualitative	Hongo and Kayanne (2009)
Kurohana reef	Yoron Island, Ryukyu Islands	NW Pacific	Drilled core	qualitative	Hongo and Kayanne (2011)
Shitooke reef	Kikai Island, Ryukyu Islands	NW Pacific	Raised reef	quantitative[‡]	Sugihara et al. (2003)
Nakaguma reef	Kikai Island, Ryukyu Islands	NW Pacific	Raised reef	quantitative[‡]	Webster et al. (1998)
Reef crest and shallow lagoon sites	Okinotori Island, Japan	NW Pacific	Drilled core	qualitative	Kayanne et al. (2012)
Ngemelis reef	Babeldaob Island, Palau Islands	NW Pacific	Drilled core	qualitative	Hongo and Kayanne (2011)
Huon Peninsula	Papua New Guinea	SW Pacific	Raised reef	qualitative	Nakamori et al. (1995b)
Huon Peninsula	Papua New Guinea	SW Pacific	Raised reef	quantitative[‡]	Pandolfi et al. (2006)
Paluma Shoals	Great Barrier Reef	SW Pacific	Drilled core	quantitative[§]	Perry et al. (2008)
Ribbon Reef 5 and Boulder Reef	Great Barrier Reef	SW Pacific	Drilled core	qualitative	Webster and Davies (2003)
Islets Kendec, Bayes, and Amédée	New Caledonia	SW Pacific	Drilled core	quantitative[§]	Hongo and Wirrmann (2015)
Tasmaloum	Vanuatu	SW Pacific	Drilled core	qualitative	Cabioch et al. (1998)
Papeete	Tahiti Island, Society Islands	SE Pacific	Drilled core	qualitative	Montaggioni et al. (1997)

[†] Measured thickness of coral layer.
[‡] Measured projected area of corals.
[§] Counts of coral pieces (based on presence/absence data).