

Coral reefs at 34°N, Japan: Exploring the end of environmental gradients

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ABSTRACT

We describe the architecture and development of the highest latitude coral reefs currently known on Earth, located in Japan at 34°N. The reefs are distributed within turbid inner bays and undergo winter sea-surface temperatures (SSTs) that fall to 13 °C, well below the generally accepted lower limit (18 °C in winter) of tropical coral reef formation. Despite low SSTs and high turbidity, coring indicates reefs ranging to 555 cm in thickness since ca. 4.3 k.y. ago. The reefs exhibit high adaptability to this extremely marginal environment. Variability of the Tsushima Warm Current and the Asian monsoon could have affected the evolution of these reefs. The corals are dominantly faviids, in contrast to *Acropora* and *Porites* that tend to dominate low-latitude, tropical-subtropical reefs. Defining the end of the distributional range, the reefs serve as baselines for understanding coral reef distribution along SST and turbidity gradients.

INTRODUCTION

Coral reefs occur most commonly in shallow, clear, warm-water settings in low-latitude, tropical-subtropical regions. Environments having harsh conditions for coral survival (hereafter “marginal environments”) include those with low sea-surface temperatures (SSTs), low aragonite saturation states, and high turbidity (Kleypas et al., 1999; Perry and Larcombe, 2003). However, recent studies have shown that reef-building corals have high adaptability to such marginal environments (Kleypas, 1996; Manzello et al., 2008; Perry et al., 2008; Tudhope and Scoffin, 1994). The coral reefs described in these studies represent extremes in the distributional range of coral reefs along the gradients of limiting factors. Among such extreme cases, a coral reef with a minimum age of 1400 ¹⁴C yr B.P. at Iki Island, Japan (33°48'N, 129°40'E) was reported (Yamano et al., 2001). This was the northernmost coral reef ever reported and could aid in understanding the distributional range of coral reefs. However, more detailed information on the history of this reef and other examples of similar structures in comparable environmental settings are needed.

This paper presents the compositional sequence and development history of the coral reefs at Iki and Tsushima Islands, Japan, over the middle to late Holocene. We report for the first time on the reef at Tsushima, newly discovered to be the world's highest-latitude coral reef. The Tsushima reef matches the reef at Iki in compositional and structural aspects. We then discuss changes in coral reefs along spatial dimensions after establishing our study reefs at the end of the distributional range. This work

provides a standardized framework of coral reef development along environmental gradients.

FIELD SETTING AND SURFACE STRUCTURE

Communities of hermatypic corals, which can tolerate fairly low temperatures, are distributed along the temperate coasts of Japan (Yamano et al., 2011). Warm currents flowing northward along coastal Japan (Kuroshio Current and Tsushima Warm Current) help extend the distribution of corals into temperate areas. Coral communities dominated by *Favia* and *Echinophyllia* have been found in low- to moderate-energy inner bays of Iki and Tsushima Islands (Sugihara et al., 2009). The islands are composed of Tertiary (Oligocene–Early Miocene) sedimentary rocks (Fig. 1) and nearby SSTs range from 13.5 °C (February–March) to 26.6 °C (August) on average (Yamano et al., 2001). SSTs below 14 °C occur from February to March almost every year. The winter SSTs are markedly below the generally accepted lower SST limit (18 °C in winter) of tropical coral reef formation. These corals also often undergo high turbidity caused by terrestrial soil input from local runoff. During the rainy and stormy season from June through October, chronic high turbidity would be expected due to the high amount of precipitation and resuspension of sediments by typhoons.

In spite of this extremely marginal (i.e., low SST and high turbidity) setting, large mounds covered with live corals occur at Kurosaki, Iki Island (33°48'N, 129°40'E). One of the mounds was shown to be a result of coral accumulation (Yamano et al., 2001). A literature search, interviews of local residents, and examination

of aerial photographs indicated the existence of additional mounds at Senoura, Tsushima Island (34°25'N, 129°16'E), 70 km north of Kurosaki (Fig. 1). Senoura and Kurosaki have similar geomorphic zonation and coral communities (Fig. 1C; Sugihara et al., 2009). These coral communities are within the same cluster based on a global-scale analysis of coral community structure (Wicks et al., 2010).

METHODS

We collected one core from Kurosaki (three cores were taken there by Yamano et al., 2001), and two cores from the top of mounds at Senoura along transects that exhibit clear geomorphic and ecological zonation (Fig. 1C). Following the methods in Yamano et al. (2001), a portable underwater drilling system (Geoact Co. Ltd., Japan) driven by compressed air (Adachi and Abe, 2003) was used to minimize damage to living corals.

Loose sediments in the cores, along with surface sediments close to the core locations, were sieved through a 63 μm mesh to determine mud contents. Corals in the cores were identified at generic and/or species levels when skeletal features of corallites were preserved. Growth orientation and preservation of surface structure were examined to determine whether corals were in situ. Dating (¹⁴C) was conducted on in situ coral specimens that showed no evidence of diagenetic alteration by X-ray diffraction analysis. Age data were corrected for isotopic fractionation and calibrated (cal) to calendar yr before present using the software Calib (ver. 6; <http://calib.qub.ac.uk/calib/>) based on the Marine09 data set and the local reservoir effect (ΔR) of -154 ± 35 yr for southern Korea (Kong and Lee, 2005). For internal consistency, the ¹⁴C ages reported in Yamano et al. (2001) were also subjected to the same correction. The ages were expressed as 1σ error ranges.

RESULTS

The core from Kurosaki had a total length of 555 cm and the 2 cores from Senoura had lengths of 478 cm and 525 cm. One of the cores from Senoura extended through the Holocene sequence and encountered fragments of mudrock, probably from Tertiary bedrock. No Pleistocene carbonate sequence was found.

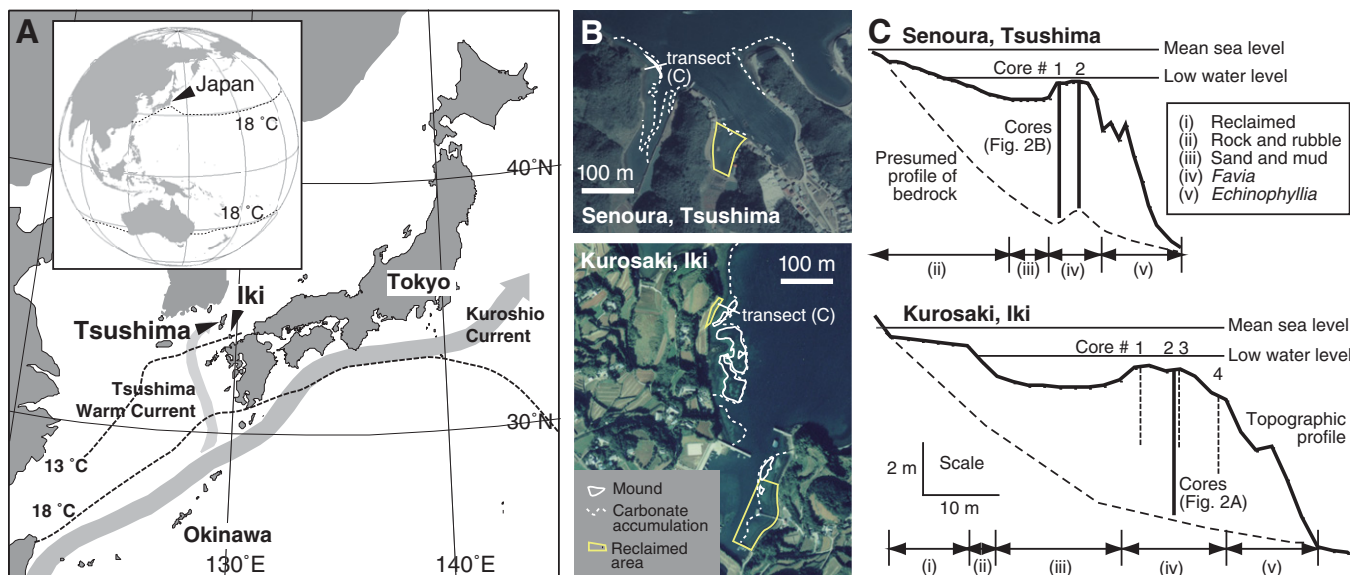


Figure 1. A: Location of Iki and Tsushima Islands. Isolines are for winter sea-surface temperatures (SSTs). **B:** Aerial photographs taken in 1986 and 1977 for Kurosaki and Senoura, respectively, showing extent of mounds and carbonate accumulation. **C:** Topographic profiles and zonation and location and number of cores. Bold solid lines—this study; dashed lines—Yamano et al. (2001).

Considering the bedrock slope inferred from topographic profiles, the other two cores are thought to have recovered nearly the entire Holocene sequence (Fig. 1C), but the three cores of Yamano et al. (2001) did not recover the entire Holocene sequence. All of the cores from Kurosaki and Senoura were dominated by corals and mud and have similar structure. Throughout the cores, other calcified organisms (mostly mollusks) accounted for <10% of total skeletal grains. Encrusting coralline algae were not found. Visible cementation was absent from all of the core materials.

The internal structure observed in the cores was divided into two distinct units, a lower unit and an upper unit, based on coral abundance and species determinations (Fig. 2). These units were also observed in the three cores of Yamano et al. (2001). The lower unit was characterized by mud and fresh fragments of diverse coral species that preserved the skeletal morphology of coral-lite surfaces (*Cyphastrea japonica*, *C. serailia*, *Echinophyllia aspera*, *Favia speciosa*, *Favites abdita*, *Hydnophora exesa*, and *Lithophyllon undulatum*). The proportion of in situ colonies of *F. speciosa* and *Cyphastrea* spp., which showed clear upward growth orientation, was <10%. On average, the dominant coral species in this unit included *Cyphastrea* spp., with minor amounts of *E. aspera*, *F. speciosa*, and *L. undulatum*. The bottom portion of this unit is characterized by the presence of fresh fragments of *E. aspera* and *L. undulatum* overlying in situ colonies of *F. speciosa* and *Cyphastrea* spp. at the core bottom. Mud content in this unit ranged from 3% to 38%. The upper unit occurred above 0.5–2.5 m depth from the core top, i.e., <2–4 m below present-day mean sea level (MSL). This unit was char-

acterized by a predominance of in situ colonies of *F. speciosa*, occupying 50%–70% of the core volume. Mud was found between the colonies, and mud content ranged from 3% to 51%.

At Kurosaki, the age of the core bottom was 2788–2703 cal yr B.P. at 543 cm below the core top. At Senoura, the bottom ages for the two cores were 4371–4213 cal yr B.P. at 525 cm and 1707–1581 cal yr B.P. at 487 cm (Fig. 2). The bottom portion of the lower unit showed a slow (~0.3 m/k.y.) growth rate before 1700 cal yr B.P. A faster growth rate (~3 m/k.y.) was observed in the upper part of the lower unit (Fig. 3). The upper unit showed an overall upward growth rate of ~2 m/k.y.

DISCUSSION

Holocene Reef Evolution

The mounds at Kurosaki and Senoura satisfy Braithwaite's (1973) definition of a coral reef: a structure that (1) has risen appreciably above the seafloor, (2) is relatively wave resistant, (3) has frame-building organisms, and (4) is characterized by an ecological zonation. In addition to these features, the mounds exhibit vertical accretion by corals and extensive spatial extents (Fig. 1), further supporting their classification as framework coral reefs. The mound at Senoura at Tsushima Island is therefore the highest-latitude coral reef on Earth, replacing the Kurosaki coral reef reported in Yamano et al. (2001).

A depth-age plot of the coral reefs shows a catch-up evolution pattern such that coral growth postdates the stabilization of sea level (Fig. 3). Sea levels in this region reached ~0.6 m below the present level ca. 7.0 k.y. ago and then rose gradually to the present level (Nakada et al.,

1994). The initiations of the Kurosaki and Senoura reefs occurred between 4.3 and 2. k.y. ago at depths of ~7 m below MSL with initial settlement by faviids, represented by *Favia speciosa* and *Cyphastrea* spp. (Figs. 2 and 3). Subsequently, the coral community was replaced by *Echinophyllia aspera* and *Lithophyllon undulatum* until 1.7 k.y. ago. Vertical reef growth was slow at ~0.3 m/k.y. at this stage of development, according to the two cores from Senoura (cluster A in Fig. 3).

The initiation and evolution patterns of the reefs can be explained by SST and turbidity, which are affected by the Tsushima Warm Current (TWC) and the Asian monsoon, respectively. Influx variability of the TWC was inferred from fossil assemblages of mollusks and diatoms in the Japan Sea (Koizumi, 2008; Matsushima, 2010). During the Holocene, a strong influx of the TWC into the Japan Sea first occurred ca. 8.0 k.y. ago, causing the first warming period in the Tsushima–Korea Strait region. However, higher precipitation caused by a stronger monsoon in the mid-Holocene in this region (ca. 6.0 k.y. ago; An et al., 2000) could have caused high turbidity that prevented coral settlement. The peak of the Asian monsoon shifted southward (An et al., 2000) and the second strong influx of the TWC occurred ca. 5.5 k.y. ago (Matsushima, 2010). These changes could have permitted coral settlement. The influx weakened ca. 2.0 k.y. ago (Matsushima, 2010), which could have caused the slow growth rate (cluster A in Fig. 3).

Faster upward reef growth of ~3 m/k.y. occurred after 1.7 k.y. ago with the shift of dominant species to *Cyphastrea* spp. (cluster B in Fig. 3), possibly in response to an increase in TWC influx ca. 1.5 k.y. ago (Matsushima,

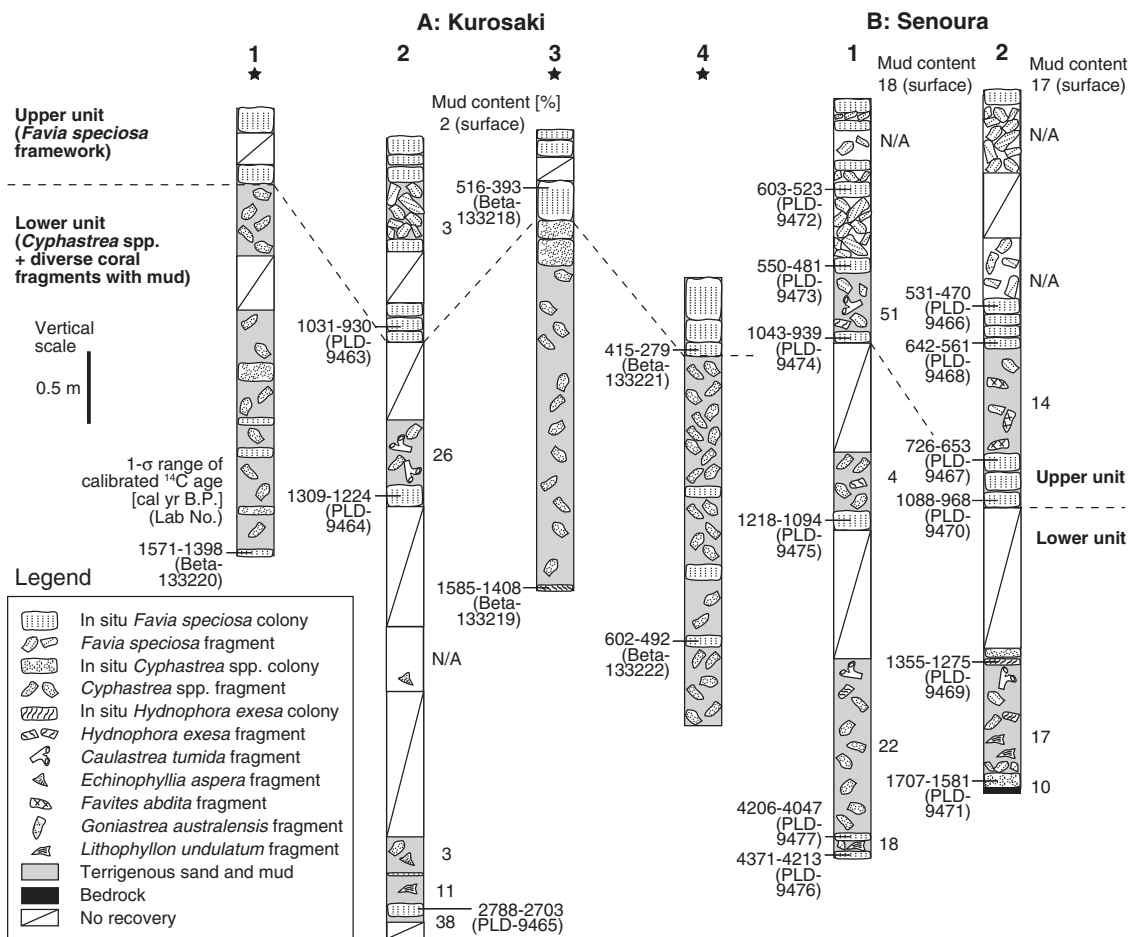


Figure 2. Core logs, sedimentary units, and ages (laboratory numbers in parentheses). A: Kurosaki. B: Senoura. Stars indicate cores of Yamano et al. (2001). Note that only dominant species are described for cores of Yamano et al. (2001) following description, although other species could have been included as found in cores collected in this study (Kurosaki-3, Senoura-1, and Senoura-2).

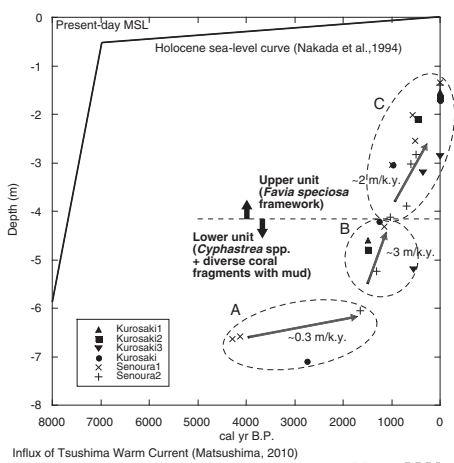


Figure 3. Comparison of relative sea-level curve from Nakada et al. (1994) and Tsushima Warm Current influx (Matsushima, 2010) with age-depth data derived from cores (^{14}C calibrated yr B.P.). Radiometric counting errors (1σ) are smaller than width of symbols. Clusters A–C were based on sedimentary structure and ages (see text). MSL—mean sea level.

2010). After 1.0 k.y. ago., when reef growth reached ~4 m below MSL, the species changed to *F. speciosa* and the vertical growth rate decreased to ~2 m/k.y. (cluster C in Fig. 3). This change could be due to shallowing, considering

that the modern distribution of *F. speciosa* is limited to depths of <4 m below MSL (Fig. 1C).

Reefs at the End of the Distributional Range

Although fluctuations in TWC influx could have significantly affected reef evolution, SSTs in the warmer periods were only 1–2 °C above those at present (Koizumi, 2008), meaning that SSTs remained extremely low for coral reef development. In addition to low SST, the reefs were probably also affected by high turbidity because mud contents in core and surface sediments (Fig. 2) were similar to those at other turbid, inner bay settings that showed 10%–50% (Perry et al., 2008) and 2%–55% (Tudhope and Scoffin, 1994) mud contents in core and surface sediments.

Thus, these reefs can be regarded as being at the end of the distributional range of coral reefs along SST and turbidity gradients. We present a simple schematic model that can provide baselines for understanding framework coral reef distribution along environmental gradients (Fig. 4). In this model, the aragonite saturation state (Ω) is treated as dependent on SST (Kleypas et al., 1999), and thus SST and Ω are given together on the vertical axis (i.e., latitude). Whereas an open-water environment generally creates a clear and moderate- to high-energy

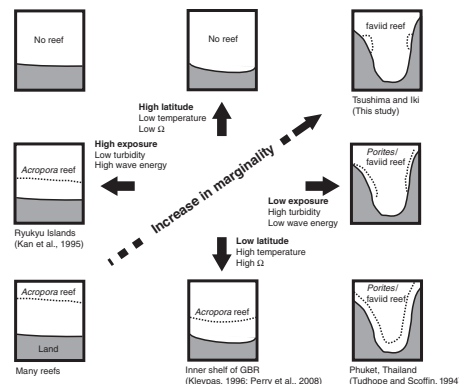


Figure 4. Conceptual model addressing framework coral reef distribution according to sea-surface temperature (SST) and turbidity gradients, with representative examples (see text for details). Given the biogeography of corals, this model would be most applicable to western Pacific region. For simplification, we considered turbidity as function of geomorphology (exposure) because it is a product of sediment input and removal (see Woolfe and Larcombe, 1999). Note that model does not consider specific environments not caused by environmental gradient. For example, upwelling could cause low SST and low aragonite saturation state (Ω) even in low latitudes, resulting in poor development of coral reefs (Manzello et al., 2008; Perry and Larcombe, 2003). GBR—Great Barrier Reef.

setting, an inner bay environment tends to be a turbid and low-energy setting. We thus regarded turbidity and energy as one variable along the horizontal axis (i.e., degree of exposure).

Tropical coral reefs in clear water and high-to moderate-energy settings are constructed mainly by *Acropora* (e.g., Hongo, 2012), but an increase in turbidity in response to a decrease in exposure, shown as a change along the horizontal axis, results in the dominance of *Porites* and faviids (Tudhope and Scoffin, 1994). Along the vertical axis, a decrease in SST and Ω in response to increasing latitude reduces the spatial extent of the reefs (Kan et al., 1995; Nakai, 1990), and at higher latitudes no coral reef formation would be expected in a high-energy, low-SST setting. This could be a result of poor cementation due to low Ω (see Manzello et al., 2008) as well as an absence of binding organisms such as coralline algae, both of which were noted in our cores. These factors allow the removal of colonies exposed to high-energy water, as high-energy waves were observed to remove coral colonies in an open bay at high latitude (32°10'N), resulting in no coral reef formation (Nozawa et al., 2008). The only possible setting for coral reef formation at high latitudes is an inner bay. Although turbidity is high, coral reefs can be formed by faviids, as we show here.

CONCLUSIONS

We have described the existence of faviid coral reefs in an extremely marginal setting, which could represent the limit of the coral reef developmental range along SST and turbidity gradients, to understand structural changes of coral reefs along environmental gradients. Several similar mounds were present in the bays, although regrettably some of them were reclaimed during port construction in the 1980s (Fig. 1B). The results suggest the possible ubiquitous occurrence of coral reefs in the study areas, further supporting these reefs as a general feature at the end of the distributional range. Analogues of these reefs may have occurred in marginal settings in the geological past, such as during the last glacial maximum (Sasaki et al., 2006) and the mid-Holocene (Veron, 1992). These structures might be worth reexamining in light of our study.

Coral reefs in high-latitude settings could be changing in the face of recent and future environmental changes. Warm-water species (*Acropora solitaryensis*), which were not found in our cores, settled within the past 20 yr at a site close to Senoura (Yamano et al., 2011). Thus, our results also suggest that historic coral community data archived in the reef cores at high latitudes could serve as baselines for assessing the consequences of rapidly warming seas.

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