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Episodic coral growth in China's subtropical coral communities linked to broad-scale climatic change

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Abstract :

Evidence from the fossil coral record has shown that coral assemblages were able to extend their geographical range to higher latitudes during past global warming events. In the face of future global warming scenarios, we investigate the potential for China's subtropical coral communities to act as a refuge for corals as ocean temperatures continue to warm. Using uranium-thorium dating to chronologically constrain the age of dead corals, we reveal two distinct periods of coral growth between 6.85 and 5.51 ka B.P. and 0.11 to -0.05 ka B.P. (relative to A.D. 1950). The former coincides with the mid–Holocene Warm Period when temperatures in South China were ~1–2 °C warmer than present. Very few ages (13%) were obtained for the ~5.6 k.y. that followed. An increased frequency of corals with 230Th ages dated to the past century suggests an increase in abundance coinciding with rising global temperatures. Nevertheless, modern monitoring programs have reported a recent dramatic decline in coral cover over the past 34 yr attributable to human influences. Our results suggest that although coral communities existed around the subtropical islands of Daya Bay (southeast China) in the past, their continued presence in the region largely depends on appropriate management of the adjacent coastline and coupled ocean-atmosphere conditions similar to those experienced in the mid-Holocene.

INTRODUCTION

With warm-water bleaching events adversely affecting many reef ecosystems in recent years, reef scientists have increasingly focused on the concept of higher-latitude environments acting as a potential refuge for corals in the face of climate change (~~van Hooidonk et al., 2013; Cacciapaglia and Woesik, 2015;~~e.g., Kavousi and Keppel, 2018). This idea is not as far reaching as it seems, with numerous terrestrial, marine and freshwater species already documented to have altered their distributions in response to recent warming (Chen et al., 2011). It therefore seems logical to protect potential refuges to foster ecosystem resilience by further mitigating anthropogenic impacts (Beger et al., 2014).

Arguably, there are many complex interacting factors (e.g., competition, local environmental changes) that may contribute toward a change in a species' distribution not directly related to climate. Furthermore, there is the uncertainty of not knowing whether certain species will (re)settle at their new location, and there is a lack of knowledge about how species have responded to past climate change events (Beger et al., 2014). Fortunately, examination of the fossil record for species found outside their extant range can provide a useful analogue to understand deep-time dynamics that may assist with predicting their response to warming in the future (Precht and Aronson, 2004; Black et al. 2014). For example, the northern range expansion of two species of *Acropora* spp. in the Caribbean over the past 40 yr, attributed to warming sea temperatures, was supported by the presence of fossil *Acropora*-dominated reefs in the early to mid-Holocene at higher latitudes in the same region (Precht and Aronson, 2004). ~~Also known as the Holocene Warm Period (HWP) or Holocene Climatic Optimum, this time period offers a means by which to evaluate potential climate refuges, with global mean annual temperatures at ca. 8–6 ka of ~0.7 °C higher than for pre-industrial conditions (Marcott et al., 2013).~~ Other relict fossil reefs that grew at higher latitudes during ~~this time~~the Holocene Warm Period (HWP; ca. 8-6 ka)~~ period~~ have also been found around the globe (Lighty et al., 1978; Veron, 1992; Woodroffe et al., 2010; Lybolt et al., 2011) and during earlier warm periods, such as the Last Interglacial (135–118 ka; e.g., Greenstein and Pandolfi, 2008).

Adjacent to mainland China, the range of modern reef-building coral species extends from Hainan Island (~18°8′N–20°8′N) in the south, where conditions are suitable for the development of ‘true’ reef systems, all the way north to the coral communities of Dongshan Bay (23°43′N–23°54′N). At their northern limits, the history of these coral communities in response to environmental change over long time periods remains unknown and, as a result, their potential to act as a climate refuge remains enigmatic. Here we use multi-collector–inductively coupled plasma–mass spectrometry (MC-ICP-MS) uranium-thorium (U-Th) dating to chronologically constrain the age of surficial dead coral material ~~(termed ‘death assemblage’; Greenstein and Pandolfi, 1997)]~~ obtained from four subtropical~~ (Belda et al., 2014)~~ coral communities in and around Daya Bay, southeast China (22°27′N–22°36′N) to understand coral reef dynamics in this region over millennia and to compare current and past climatic and environmental conditions with coral building episodes.

METHODS

Our study was conducted on the protected leeward sides of Xiaolajia and Dalajia Islands within Daya Bay, Zhouzaitou Island within Daao Bay, and Sanmen Island, China, in October 2015 (Fig. 1; see Table DR1 in the GSA Data Repository[1]). Corals can be found in non-accreting, patchily distributed communities growing on basement rock and sand (Chen et al., 2009). Between A.D. 1985 and 2005, sea-surface temperatures (SSTs) in Daya Bay rose steadily from an annual average of ~18 °C (1988) to ~21 °C (2005) at a rate of 0.07 °C yr^{-1} (Yu et al., 2010). Since 2005, annual mean SSTs similarly derived from nighttime satellite data at 4 km resolution from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) on the Aqua satellite approximate 24 °C, with minimum and maximum monthly mean temperatures of ~15 °C and ~30 °C, respectively (Fig. ~~3A~~2A; Fig. DR1). ~~Coral death assemblage~~Dead corals were collected haphazardly by hand on SCUBA at the sediment-water interface along a gradient of increasing depth (between 1.3 and 5.8 m depth relative to mean sea level [MSL] at each site where present (~~[~~Table DR1~~]~~). ~~Samples were dried and photographed at the Guangzhou Institute of Geochemistry (China) where a~~ A small subsample from each colony (5 cm^3) was then prepared for ~~, cut using a diamond blade saw, was shipped to the Radiogenic Isotope Facility, The University of Queensland (Australia) for sample preparation and~~ U-Th dating using a Nu Plasma I High Resolution MC-ICP-MS following the procedures described by Clark et al. (2014~~a, 2014b~~) at the Radiogenic Isotope Facility, The

University of Queensland, Australia (Fig. DR2; see the Data Repository for further details).

RESULTS AND DISCUSSION

Understanding past coral community distributions and their response to environmental change is important for making predictions on how modern systems will respond in the future. This is the first study to chronologically constrain the age distribution of surficial dead corals~~ death assemblages~~ collected within and around Daya Bay. The results from 92 ^{230}Th age data obtained from the corals revealed two distinct populations of ages centered at 5.8 and –0.02 kyr B.P. (see the Data Repository for further detail), suggesting that corals were more abundant during these time periods compared to the 5.6 k.y. in between, where very few ages (13~~7~~%) were obtained. Here we discuss factors that may promote or prevent coral communities to flourish (e.g., substrate availability, nutrient levels, ~~hydrodynamic energy, ~~coral recruitment (~~[~~Montaggioni, 2005)~~]~~, and more recently anthropogenic disturbances (~~[~~Pandolfi et al., 2003~~]~~), particularly for those located in marginal and inshore environments such as Daya Bay.

Sea-Level Rise and Fall as a Driver for Episodic Reef Growth?

Greater volumes of coral material dating to the mid-Holocene is believed to reflect prolific reef growth as reefs kept up (or caught up) with rising sea level following the last deglaciation, while the absence of material thereafter is thought to reflect limited vertical accommodation space since sea level stabilized and fell slightly (Montaggioni, 2005). The most comprehensive compilation of sea-level records for the~~ East~~ Guangdong coastal area suggests that sea level rose to present day mean sea level at ca.

6.8-5.8 calibrated (cal.) kyr B.P. based on radiocarbon dates, increasing to +1.0/–1.5 m at ca. 5.0 cal. kyr B.P. before gradually declining toward the present-day level (Fig. ~~3C~~2C; Zong, 2004). ~~The sea-level curve for West Guangdong further south followed a similar pattern, albeit reaching present-day height slightly earlier (6.8 cal. kyr B.P.) and remaining relatively stable since (Fig. 3C). Zong (2004) attributes this spatial variation in the timing and height of the highstand for these areas to different coastal geometries and geological processes, with the apparent 1 m higher sea level for East Guangdong a result of tectonic uplift due to its close proximity to a plate boundary. Overall,~~ While sea level appears to have remained relatively stable for the east coast of China since the mid-Holocene ~~and suggests that coral communities were not limited by vertical accommodation space caused by a subsequent sea-level fall.~~

~~However~~, the mixture of sea-level indicators (e.g., beach rock, sediments, coral) and the inherently large age errors used in Zong's (2004) model make it difficult to know whether oscillating or subtle falls in sea level (such as that seen at ca. 4.0 kyr B.P. for West Guangdong) may have played a role in the presence and absence of coral communities around Daya Bay. Evidence for oscillating sea levels has been found to occur during two major periods at Big Wave Bay, Hong Kong Island, ~5.9 and ~1.8 cal kyr B.P. (Baker et al., 2003), Leizhou Peninsula at 7.2–5.0 and 2.5–1.5 cal. kyr B.P. (Zhao and Yu, 2002~~; Yu et al., 2009~~) and more broadly at other far field locations such as Indonesia, Bangladesh, Kodakara Island in the northwest Pacific, and Australia (Leonard et al., 2018), albeit at different time periods.

For Daya Bay, modern living coral communities were found in the exact same environments as their relict counterparts, well below the upper limits for coral growth (within ±25 cm of mean low water spring ~~[MLWS]~~ tide level; Hopley, 1986) determined to be 0.5 m lowest astronomical tide ~~(LAT)~~ at nearby Quarry Bay, Hong Kong, in 2015 (Table DR3). We also found no significant relationship ($R^2 = 0.006$, $P = 0.473$) between coral age and sampling depth, suggesting very little influence of a lowering sea level on coral distribution over time. Therefore, mechanisms outside the constraints of sea level are likely to have been responsible for the low abundance of corals around Daya Bay between 5.8 and –0.02 kyr B.P.

Broad-Scale Climatic Change Linked to Reef Growth and Demise

The presence of corals during the mid-Holocene not only coincides with a heightened sea level, but also the stable, warmer and wetter HWP where proxy SST records reveal annual mean temperatures up to 2 °C warmer in South China and neighboring seas compared to the present day (Fig. ~~3A~~2A). This period was characterized by heightened solar insolation (Fig. ~~3B~~2B), which in turn affected ocean-atmosphere interactions, particularly heat and moisture transport in the tropical Pacific Ocean (Selvaraj et al. 2008). Warmer waters were transported northwards from the South China Sea (SCS) and the Indo-Pacific warm pool to the mid-latitudes via the northern SCS circulation pattern and the Kuroshio current as a result of enhanced East Asian Monsoonal (EAM) winds, reduced El Niño–Southern Oscillation (ENSO) and the northward positioning of the intertropical convergence zone (ITCZ) (~~Hu et al., 2000;~~ Selvaraj et al., 2008~~; Nan et al., 2015~~), bringing with it coral larvae from tropical coral reefs (Veron, 1992~~; Iryu et al., 2006~~).

Following the HWP, there was a reduction in solar insolation from ca. 5.5 kyr B.P. resulting in the southward migration of the ITCZ and intensification of ENSO

(Selvaraj et al., 2008). This event also resulted in a sharp drop in EAM intensity and a long-term decline in mean SSTs, accompanied by a similar decrease in moisture to mainland China (Figs. ~~3A~~2A,~~3B~~2B,and ~~3D~~2D). Proxy reconstructions of SSTs from massive *Porites* colonies in the northern SCS suggest a 1–2 °C lowering of mean SSTs compared to the late 20th century during this time (Yu et al. 2005; Fig. ~~3A~~2A). At higher latitudes around Daya Bay, a similar lowering of SST may have pushed corals past their thermal tolerance limit. Geochemical evidence of cold water bleaching from the fossil record suggests that this was indeed not an unusual phenomenon even during the HWP (Yu et al., 2004). It is therefore plausible that an increase in mortality associated with ~~cold water~~thermal bleaching in winter, together with a reduction in larval transport to waters off Guangdong Province as a result of weakened monsoon activity and heat transport from the tropics, may have severely affected the resilience of coral communities in the region between 5.8 and –0.02 kyr B.P.

Similar conditions may have also led to the decline in *Acropora* spp. corals along the east coast of Florida (Precht and Aronson, 2004) where paleo-reconstructions of ocean currents revealed a decrease in the transport of Caribbean surface waters by the warm Loop Current into the western Gulf of Mexico after ca. 5 kyr B.P. as a result of orbitally forced changes in the position of the ITCZ (Poore et al., 2003). The presence of marginal coral communities during the HWP, followed by an overall decline in abundance for most of the late Holocene has also been demonstrated at Lord Howe Island, Australia (Woodroffe et al., 2010), Moreton Bay, Australia (Lybolt et al., 2011), Tateyama, Japan (Veron, 1992) and Florida, USA (Lighty et al., 1978~~; Stathakopoulos~~

~~and Riegl, 2015~~). This suggests that the temporal distribution of corals observed in this study is likely caused by climatic factors acting over broader spatial scales.

Following this sub-optimal period for coral growth, the number of corals increases dramatically from ~0.11 kyr B.P. (or ~A.D. 1840), with 67% of ^{230}Th ages dating to less than 100 yr old (Figs. ~~3A~~ 2A and ~~3D~~2D), coinciding with a rapid rise in global mean temperatures ~~from near the coolest to the warmest levels of the Holocene within the past century~~ (Marcott et al., 2013). Similar reappearances of corals outside their ‘normal’ geographic range have also been observed in recent years in the Caribbean, Australia, and Japan attributed to global warming (Baird et al., 2012; Precht and Aronson, 2004; Yamano et al., 2011).

Current Threats and Recent Mortality

Coral communities in and around Daya Bay appear to have had a positive response to recent climatic change (mid-18th century onward following the Industrial Revolution), albeit short-lived. Since the onset of modern benthic surveys in the mid-1980s, mean coral cover has dramatically declined from 76.6% in A.D. 1983/1984 to 15.3% in 2008 (Chen et al., 2009). This has been attributed to poor environmental conditions (e.g., increased heavy metal and thermal pollution, ~~herbicides, pesticides,~~ nutrients and sediments) associated with the rapid expansion of urban development, aquaculture and industry (see Chen et al., 2009, for summary). Importantly, the return of coral communities in Daya Bay predates the local warming of seawater caused by the discharge from nuclear power plants (Yu et al., 2010). While local efforts to improve water quality in the region may bolster the resilience of communities in the face of a warming climate, recent studies have shown that the response of ocean-atmosphere interactions as a result of anthropogenic forcing may be more complex than previously thought. It is predicted that the de-coupling between warmer temperatures and a strengthened EAM prior to the twentieth century and the long-term warming of the tropical Pacific Ocean may result in a persistent ENSO-like state (Li~~, X. L.,~~ et al., 2017). This could have severe implications on ocean circulation patterns (Li~~, X. H.,~~ et al., 2017) and potentially isolate coral communities at higher latitudes, preventing them from acting as a refuge in the future. How corals will fare with the unprecedented rate of global warming also remains uncertain, with the risk that the poleward speed of warming may overtake and ecologically extirpate some or many coral species before they are able to ‘escape’ to high-latitude refugia. Yet evidence of rapid range expansions (e.g., Yamano et al., 2011~~; Serrano et al. 2013~~) suggests that there may be some capacity for corals to cope with their rapidly changing environment.

CONCLUSIONS

In summary, our findings indicate two distinct periods for coral growth during the Holocene at several inshore environments within and around Daya Bay, China. Consistent with other studies around the globe that found a higher abundance of corals both in the mid-Holocene and during more recent times, our results suggest that broad scale climatic change associated with a warmer climate largely influences the presence and absence of coral communities in subtropical locations. Our study highlights the importance of paleo-ecological studies to improve our understanding of coral dynamics in response to environmental changes and demonstrates the capacity for these subtropical reefs to act as a potential refuge in the face of a warming climate. This is largely dependent on anthropogenic activities responsible for the recent decline in coral cover being reversed and the complex factors driving ocean circulation patterns in adjacent waters continuing to provide a source of larvae.

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FIGURE CAPTIONS

Figure 1. Location of study. A: Map of China with study site (1) and location of environmental proxy data referred to in this study: Dongge and Sanbao Cave δ^{18}O rainfall proxy records (2,3)~~, Sanbao Cave δ^{18}O rainfall proxy records (3)~~, East and West Guangdong paleo-sea level (4,5)~~, West Guangdong paleo-sea level (5)~~, Hainan Island and Leizhou Peninsula Sr/Ca sea-surface temperature (SST) records (6,7)~~, Leizhou Peninsula Sr/Ca-SST records (7)~~, and east coast Japan Mg/Ca-SST records (8). Solid and dashed gray arrows represent the simplified direction of the South China Sea warm current and the Kuroshio current, respectively. B: Dead corals~~ or ‘death assemblages’~~ were collected from the leeward side of Dalajia and Xiaolajia Islands (Daya Bay), Zhouzaitou Island (Dapeng Bay), and Sanmen Island.

~~Figure 2. A: A well-preserved dead *Acropora* sp. branch from Sanmen Islands (China) dating to 6.1 ± 0.6 kyr B.P. B: *Platygyra* sp. From Dalajia (Shuazhou) Island dating to −0.057 ± 0.002 kyr B.P. Scale bar represents 1 cm.~~

Figure 2~~3~~. U-Th age data compared with broad scale paleo-environmental and -climatic data from the mid-Holocene (9 kyr B.P.) to present. A: Annual sea-surface temperature (SST, °C) reconstructed from diatom assemblages in sediment core MD01–2421, east coast Japan (IMAGES VII–WEPAMA cruise, on the R/V *Marion Dufresne*) (Koizumi,

2008) as well as SST average, maximum, and minimum obtained from *Porites* coral Sr/Ca records for samples SYO-15, SYL-1, SYL-4 (Wei et al., 2007) and SST maximum and minimum obtained from *Porites* Sr/Ca records for 1.5 ka and 2.5 ka (Yu et al., 2005). Regional SST anomaly data (±1σ uncertainty) for 90–30°N (Marcott et al., 2013) showing a clear inflection in temperature following the industrial revolution. Modern average, maximum, and minimum SSTs at 114.494–114.815°E, 22.5192–22.8433°N for A.D. 2002–2018 obtained from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) on the Aqua satellite at 4 km resolution (https://giovanni.gsfc.nasa.gov). B: Oxygen isotope ($^{18}O/^{16}O$) records, a proxy for rainfall, obtained from Sanbao speleothem SB26 and SB10 (Wang et al., 2008) and Dongge Cave speleothem (Yuan et al., 2004), together with 65°N summer insolation (Berger and Loutre, 1991). C: Corrected altitude (m) relative to modern mean sea level (MSL) obtained from various sea-level indicators from East and West Guangdong (Zong, 2004). Also shown is lowest astronomical tide (LAT, or chart datum) for Quarry Bay, Hong Kong (1.376 m below MSL). D) ^{230}Th ages obtained from 92 dead corals collected from Xiaolajia, Dalajia, Sanmen, and Zhouzaitou Islands. Age errors are smaller than the size of the symbols. Height and width of the relative probability curve reflects the number of samples dating to the same time period and associated error, respectively. Gray boxes highlight periods of weakened East Asian Monsoon activity (Selvaraj et al., 2008).

[1] GSA Data Repository item 2018xxx, Tables DR1–DR3 and Figures DR1-~~ and ~~DR3~~2~~, is available online at http://www.geosociety.org/datarepository/2018/, or on request from editing@geosociety.org.