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

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

## **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  $^{230}\text{Th}$  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.

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11 **ABSTRACT**

12 Evidence from the fossil coral record has shown that coral assemblages were able  
13 to extend their geographical range to higher latitudes during past global warming events.  
14 In the face of future global warming scenarios, we investigate the potential for China's  
15 subtropical coral communities to act as a refuge for corals as ocean temperatures continue  
16 to warm. Using uranium-thorium dating to chronologically constrain the age of dead  
17 corals, we reveal two distinct periods of coral growth between 6.85 and 5.51 kyr B.P. and  
18 0.11 to -0.05 kyr B.P. (kyr B.P. relative to 1950). The former coincides with the mid-  
19 Holocene Warm Period when temperatures in South China were ~1–2 °C warmer than  
20 present. Very few ages (13%) were obtained for the ~5.6 k.y. that followed. An increased  
21 frequency of corals with <sup>230</sup>Th ages dated to the past century suggests an increase in  
22 abundance coinciding with rising global temperatures. Nevertheless, modern monitoring

23 programs have reported a recent dramatic decline in coral cover over the past 34 years  
24 attributable to human influences. Our results suggest that although coral communities  
25 existed around the subtropical islands of Daya Bay (southeast China) in the past, their  
26 continued presence in the region largely depends on appropriate management of the  
27 adjacent coastline and coupled ocean-atmosphere conditions similar to those experienced  
28 in the mid-Holocene.

## 29 INTRODUCTION

30 With warm-water bleaching events adversely affecting many reef ecosystems in  
31 recent years, reef scientists have increasingly focused on the concept of higher-latitude  
32 environments acting as a potential refuge for corals in the face of climate change (~~van~~  
33 ~~Hooidek et al., 2013; Cacciapaglia and Woesik, 2015; e.g.,~~ Kavousi and Keppel, 2018).  
34 This idea is not as far reaching as it seems, with numerous terrestrial, marine and  
35 freshwater species already documented to have altered their distributions in response to  
36 recent warming (Chen et al., 2011). It therefore seems logical to protect potential refuges  
37 to foster ecosystem resilience by further mitigating anthropogenic impacts (Beger et al.,  
38 2014).

39 Arguably, there are many complex interacting factors (e.g., competition, local  
40 environmental changes) that may contribute toward a change in a species' distribution not  
41 directly related to climate. Furthermore, there is the uncertainty of not knowing whether  
42 certain species will (re)settle at their new location, and there is a lack of knowledge about  
43 how species have responded to past climate change events (Beger et al., 2014).  
44 Fortunately, examination of the fossil record for species found outside their extant range  
45 can provide a useful analogue to understand deep-time dynamics that may assist with

46 predicting their response to warming in the future (Precht and Aronson, 2004; Black et al.  
47 2014). For example, the northern range expansion of two species of *Acropora* spp. in the  
48 Caribbean over the past 40 yr, attributed to warming sea temperatures, was supported by  
49 the presence of fossil *Acropora*-dominated reefs in the early to mid-Holocene at higher  
50 latitudes in the same region (Precht and Aronson, 2004). ~~Also known as the Holocene~~  
51 ~~Warm Period (HWP) or Holocene Climatic Optimum, this time period offers a means by~~  
52 ~~which to evaluate potential climate refuges, with global mean annual temperatures at ca.~~  
53 ~~8–6 ka of ~0.7 °C higher than for pre-industrial conditions (Marcott et al., 2013).~~ Other  
54 relict fossil reefs that grew at higher latitudes during ~~this time~~ the Holocene Warm Period  
55 (HWP; ca. 8-6 ka) ~~period~~ have also been found around the globe (Lighty et al., 1978;  
56 Veron, 1992; Woodroffe et al., 2010; Lybolt et al., 2011) and during earlier warm  
57 periods, such as the Last Interglacial (135–118 ka; e.g., Greenstein and Pandolfi, 2008).

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

69 over millennia and to compare current and past climatic and environmental conditions  
70 with coral building episodes.

## 71 **METHODS**

72 Our study was conducted on the protected leeward sides of Xiaolajia and Dalajia  
73 Islands within Daya Bay, Zhouzaitou Island within Daa Bay, and Sanmen Island, China,  
74 in October 2015 (Fig. 1; see Table DR1 in the GSA Data Repository<sup>1</sup>). Corals can be  
75 found in non-accreting, patchily distributed communities growing on basement rock and  
76 sand (Chen et al., 2009). Between A.D. 1985 and 2005, sea-surface temperatures (SSTs)  
77 in Daya Bay rose steadily from an annual average of ~18 °C (1988) to ~21 °C (2005) at a  
78 rate of 0.07 °C yr<sup>-1</sup> (Yu et al., 2010). Since 2005, annual mean SSTs similarly derived  
79 from nighttime satellite data at 4 km resolution from NASA's **Moderate Resolution**  
80 **Imaging Spectroradiometer (MODIS) on the Aqua satellite** approximate 24 °C, with  
81 minimum and maximum monthly mean temperatures of ~15 °C and ~30 °C, respectively  
82 (Fig. ~~3A2A~~; Fig. DR1). ~~Coral death assemblage~~Dead corals were collected haphazardly  
83 by hand on SCUBA at the sediment-water interface along a gradient of increasing depth  
84 (between 1.3 and 5.8 m depth relative to mean sea level [MSL] at each site where present  
85 (~~{Table DR1}~~). ~~Samples were dried and photographed at the Guangzhou Institute of~~  
86 ~~Geochemistry (China) where a~~ A small subsample from each colony (5 cm<sup>3</sup>) was then  
87 prepared for, ~~cut using a diamond blade saw, was shipped to the Radiogenic Isotope~~  
88 ~~Facility, The University of Queensland (Australia) for sample preparation and U-Th~~  
89 dating using a Nu Plasma I High Resolution MC-ICP-MS following the procedures  
90 described by Clark et al. (2014~~a~~, ~~2014b~~) at the Radiogenic Isotope Facility, The

91 [University of Queensland, Australia](#) (Fig. [DR2](#); see the Data Repository for further  
92 details).

## 93 **RESULTS AND DISCUSSION**

94 Understanding past coral community distributions and their response to  
95 environmental change is important for making predictions on how modern systems will  
96 respond in the future. This is the first study to chronologically constrain the age  
97 distribution of surficial ~~dead~~ corals ~~death assemblages~~ collected within and around Daya  
98 Bay. The results from 92 <sup>230</sup>Th age data obtained from the corals revealed two distinct  
99 populations of ages centered at 5.8 and -0.02 kyr B.P. (see the Data Repository for  
100 further detail), suggesting that corals were more abundant during these time periods  
101 compared to the 5.6 k.y. in between, where very few ages ([137%](#)) were obtained. Here  
102 we discuss factors that may promote or prevent coral communities to flourish (e.g.,  
103 substrate availability, nutrient levels, ~~hydrodynamic energy~~, coral recruitment  
104 (~~{Montaggioni, 2005}~~), and more recently anthropogenic disturbances (~~{Pandolfi et al.,~~  
105 ~~2003}~~), particularly for those located in marginal and inshore environments such as Daya  
106 Bay.

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

108 Greater volumes of coral material dating to the mid-Holocene is believed to  
109 reflect prolific reef growth as reefs kept up (or caught up) with rising sea level following  
110 the last deglaciation, while the absence of material thereafter is thought to reflect limited  
111 vertical accommodation space since sea level stabilized and fell slightly (Montaggioni,  
112 2005). The most comprehensive compilation of sea-level records for the ~~East~~  
113 Guangdong coastal area suggests that sea level rose to present day mean sea level at ca.

114 ~~6.8-5.8 calibrated (cal.) kyr B.P. based on radiocarbon dates, increasing to +1.0/–1.5 m at~~  
115 ~~ca. 5.0 cal. kyr B.P. before gradually declining toward the present-day level (Fig. 3C2C;~~  
116 ~~Zong, 2004). The sea level curve for West Guangdong further south followed a similar~~  
117 ~~pattern, albeit reaching present-day height slightly earlier (6.8 cal. kyr B.P.) and~~  
118 ~~remaining relatively stable since (Fig. 3C). Zong (2004) attributes this spatial variation in~~  
119 ~~the timing and height of the highstand for these areas to different coastal geometries and~~  
120 ~~geological processes, with the apparent 1 m higher sea level for East Guangdong a result~~  
121 ~~of tectonic uplift due to its close proximity to a plate boundary. Overall, While~~ sea level  
122 appears to have remained relatively stable for the east coast of China since the mid-  
123 Holocene ~~and suggests that coral communities were not limited by vertical~~  
124 ~~accommodation space caused by a subsequent sea level fall.~~

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

135 For Daya Bay, modern living coral communities were found in the exact same  
136 environments as their relict counterparts, well below the upper limits for coral growth

137 (within  $\pm 25$  cm of mean low water spring ~~[MLWS]~~ tide level; Hopley, 1986) determined  
138 to be 0.5 m **lowest astronomical tide (LAT)** at nearby Quarry Bay, Hong Kong, in 2015  
139 (Table DR3). We also found no significant relationship ( $R^2 = 0.006$ ,  $P = 0.473$ ) between  
140 coral age and sampling depth, suggesting very little influence of a lowering sea level on  
141 coral distribution over time. Therefore, mechanisms outside the constraints of sea level  
142 are likely to have been responsible for the low abundance of corals around Daya Bay  
143 between 5.8 and  $-0.02$  kyr B.P.

#### 144 **Broad-Scale Climatic Change Linked to Reef Growth and Demise**

145 The presence of corals during the mid-Holocene not only coincides with a  
146 heightened sea level, but also the stable, warmer and wetter HWP where proxy SST  
147 records reveal annual mean temperatures up to  $2^\circ\text{C}$  warmer in South China and  
148 neighboring seas compared to the present day (Fig. [3A2A](#)). This period was characterized  
149 by heightened solar insolation (Fig. [3B2B](#)), which in turn affected ocean-atmosphere  
150 interactions, particularly heat and moisture transport in the tropical Pacific Ocean  
151 (Selvaraj et al. 2008). Warmer waters were transported northwards from the South China  
152 Sea (SCS) and the Indo-Pacific warm pool to the mid-latitudes via the northern SCS  
153 circulation pattern and the Kuroshio current as a result of enhanced East Asian  
154 Monsoonal (EAM) winds, reduced El Niño–Southern Oscillation (ENSO) and the  
155 northward positioning of the intertropical convergence zone (ITCZ) ([Hu et al., 2000](#);  
156 Selvaraj et al., 2008; [Nan et al., 2015](#)), bringing with it coral larvae from tropical coral  
157 reefs (Veron, 1992; [Iryu et al., 2006](#)).

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

160 (Selvaraj et al., 2008). This event also resulted in a sharp drop in EAM intensity and a  
161 long-term decline in mean SSTs, accompanied by a similar decrease in moisture to  
162 mainland China (Figs. [3A2A](#), [3B2B](#), and [3D2D](#)). Proxy reconstructions of SSTs from  
163 massive *Porites* colonies in the northern SCS suggest a 1–2 °C lowering of mean SSTs  
164 compared to the late 20<sup>th</sup> century during this time (Yu et al. 2005; Fig. [3A2A](#)). At higher  
165 latitudes around Daya Bay, a similar lowering of SST may have pushed corals past their  
166 thermal tolerance limit. Geochemical evidence of cold water bleaching from the fossil  
167 record suggests that this was indeed not an unusual phenomenon even during the HWP  
168 (Yu et al., 2004). It is therefore plausible that an increase in mortality associated with  
169 ~~cold water~~thermal bleaching in winter, together with a reduction in larval transport to  
170 waters off Guangdong Province as a result of weakened monsoon activity and heat  
171 transport from the tropics, may have severely affected the resilience of coral communities  
172 in the region between 5.8 and –0.02 kyr B.P.

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

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

184       Following this sub-optimal period for coral growth, the number of corals  
185 increases dramatically from ~0.11 kyr B.P. (or ~A.D. 1840), with 67% of <sup>230</sup>Th ages  
186 dating to less than 100 yr old (Figs. [3A-2A](#) and [3D2D](#)), coinciding with a rapid rise in  
187 global mean temperatures ~~from near the coolest to the warmest levels of the Holocene~~  
188 ~~within the past century~~ (Marcott et al., 2013). Similar reappearances of corals outside  
189 their ‘normal’ geographic range have also been observed in recent years in the Caribbean,  
190 Australia, and Japan attributed to global warming (Baird et al., 2012; Precht and  
191 Aronson, 2004; Yamano et al., 2011).

## 192 **Current Threats and Recent Mortality**

193       Coral communities in and around Daya Bay appear to have had a positive  
194 response to recent climatic change (mid-18<sup>th</sup> century onward following the Industrial  
195 Revolution), albeit short-lived. Since the onset of modern benthic surveys in the mid-  
196 1980s, mean coral cover has dramatically declined from 76.6% in A.D. 1983/1984 to  
197 15.3% in 2008 (Chen et al., 2009). This has been attributed to poor environmental  
198 conditions (e.g., increased heavy metal and thermal pollution, ~~herbicides, pesticides,~~  
199 nutrients and sediments) associated with the rapid expansion of urban development,  
200 aquaculture and industry (see Chen et al., 2009, for summary). Importantly, the return of  
201 coral communities in Daya Bay predates the local warming of seawater caused by the  
202 discharge from nuclear power plants (Yu et al., 2010). While local efforts to improve  
203 water quality in the region may bolster the resilience of communities in the face of a  
204 warming climate, recent studies have shown that the response of ocean-atmosphere

205 interactions as a result of anthropogenic forcing may be more complex than previously  
206 thought. It is predicted that the de-coupling between warmer temperatures and a  
207 strengthened EAM prior to the twentieth century and the long-term warming of the  
208 tropical Pacific Ocean may result in a persistent ENSO-like state (Li, ~~X. L.~~, et al., 2017).  
209 This could have severe implications on ocean circulation patterns (Li, ~~X. H.~~, et al., 2017)  
210 and potentially isolate coral communities at higher latitudes, preventing them from acting  
211 as a refuge in the future. How corals will fare with the unprecedented rate of global  
212 warming also remains uncertain, with the risk that the poleward speed of warming may  
213 overtake and ecologically extirpate some or many coral species before they are able to  
214 ‘escape’ to high-latitude refugia. Yet evidence of rapid range expansions (e.g., Yamano et  
215 al., 2011; ~~Serrano et al. 2013~~) suggests that there may be some capacity for corals to cope  
216 with their rapidly changing environment.

## 217 **CONCLUSIONS**

218 In summary, our findings indicate two distinct periods for coral growth during the  
219 Holocene at several inshore environments within and around Daya Bay, China.  
220 Consistent with other studies around the globe that found a higher abundance of corals  
221 both in the mid-Holocene and during more recent times, our results suggest that broad  
222 scale climatic change associated with a warmer climate largely influences the presence  
223 and absence of coral communities in subtropical locations. Our study highlights the  
224 importance of paleo-ecological studies to improve our understanding of coral dynamics  
225 in response to environmental changes and demonstrates the capacity for these subtropical  
226 reefs to act as a potential refuge in the face of a warming climate. This is largely  
227 dependent on anthropogenic activities responsible for the recent decline in coral cover

228 being reversed and the complex factors driving ocean circulation patterns in adjacent  
229 waters continuing to provide a source of larvae.

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## 386 **FIGURE CAPTIONS**

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

397  
398 ~~Figure 2. A: A well-preserved dead *Acropora* sp. branch from Sanmen Islands (China)~~  
399 ~~dating to  $6.1 \pm 0.6$  kyr B.P. B: *Platygyra* sp. From Dalajia (Shuazhou) Island dating to~~  
400  ~~$-0.057 \pm 0.002$  kyr B.P. Scale bar represents 1 cm.~~

401

402 Figure 23. U-Th age data compared with broad scale paleo-environmental and -climatic  
403 data from the mid-Holocene (9 kyr B.P.) to present. A: Annual sea-surface temperature  
404 (SST, °C) reconstructed from diatom assemblages in sediment core MD01–2421, east  
405 coast Japan (IMAGES VII–WEPAMA cruise, on the R/V *Marion Dufresne*) (Koizumi,

406 2008) as well as SST average, maximum, and minimum obtained from *Porites* coral  
407 Sr/Ca records for **samples** SYO-15, SYL-1, SYL-4 (Wei et al., 2007) and SST maximum  
408 and minimum obtained from *Porites* Sr/Ca records for 1.5 ka and 2.5 ka (Yu et al., 2005).  
409 Regional SST anomaly data ( $\pm 1\sigma$  uncertainty) for 90–30°N (Marcott et al., 2013)  
410 showing a clear inflection in temperature following the industrial revolution. Modern  
411 average, maximum, and minimum SSTs at 114.494–114.815°E, 22.5192–22.8433°N for  
412 A.D. 2002–2018 obtained from NASA’s **Moderate Resolution Imaging**  
413 **Spectroradiometer (MODIS) on the** Aqua **satellite** at 4 km resolution  
414 (<https://giovanni.gsfc.nasa.gov>). B: Oxygen isotope ( $^{18}\text{O}/^{16}\text{O}$ ) records, a proxy for  
415 rainfall, obtained from Sanbao speleothem SB26 and SB10 (Wang et al., 2008) and  
416 Dongge Cave speleothem (Yuan et al., 2004), together with 65°N summer insolation  
417 (Berger and Loutre, 1991). C: Corrected altitude (m) relative to modern mean sea level  
418 (MSL) obtained from various sea-level indicators from East and West Guangdong (Zong,  
419 2004). Also shown is lowest astronomical tide (LAT, or chart datum) for Quarry Bay,  
420 Hong Kong (1.376 m below MSL). D)  $^{230}\text{Th}$  ages obtained from 92 dead corals collected  
421 from Xiaolajia, Dalajia, Sanmen, and Zhouzaitou Islands. Age errors are smaller than the  
422 size of the symbols. Height and width of the relative probability curve reflects the  
423 number of samples dating to the same time period and associated error, respectively.  
424 Gray boxes highlight periods of weakened East Asian Monsoon activity (Selvaraj et al.,  
425 2008).  
426

427 <sup>1</sup>GSA Data Repository item 2018xxx, Tables DR1–DR3 and Figures DR1–~~and~~ DR~~3~~2, is  
428 available online at <http://www.geosociety.org/datarepository/2018/>, or on request from  
429 [editing@geosociety.org](mailto:editing@geosociety.org).