

RESEARCH ARTICLE

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Key Points:

- Modern sea-level rise is switching on reef growth that has previously been dormant due to limited accommodation space over 5,000 years
- Recolonization of the marginal reef flat is dominated by free-living *Porites compressa* colonies with distinctive living strategies
- Inshore coral reefs in highly degraded environments may change species assemblages in response to sea-level rise but maintain reef growth

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Recolonization of Marginal Coral Reef Flats in Response to Recent Sea-Level Rise

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Abstract In an era of global change and rising sea levels, the capacity for inshore reefs to survive is increasingly unclear. We report on recent colonization of an inshore reef-flat environment at Sanya Bay, northern South China Sea, in shallow, muddy, eutrophic, and turbid conditions, which are widely viewed as marginal for sustained coral growth. U-Th dating of fossil *Acropora* substrate indicated that the reef flat has existed in a dormant state since ~5,400 years BP, with no vertical space available to accommodate coral expansion. Our surveys revealed that populations of free-living *Porites compressa* have recolonized the reef flat through asexual fragmentation, covering $13.9 \pm 1.3\%$ of reef-flat substrates. Age-frequency analysis indicated that the majority (86%) of *P. compressa* colonies were less than 30 years old. Analysis of long-term sea-level data indicated that recent recolonization of the reef flat occurred in response to a sea-level rise of 16.2 ± 0.6 cm over the past 30 years (1987–2016). Modern sea-level rise at Sanya Bay appears to have turned on reef growth which has existed in a senescent turned off state for over five millennia. The asexual life history strategy of *P. compressa* colonies, which involves forming free-living colonies (*coralliths*), allows them to overcome turbid environmental conditions that are otherwise adverse to sexual recruitment. Our results provide novel insight into the response of marginal habitats to sea-level rise, and suggest that coral cover on degraded coral reef flats could increase under future sea-level rise, albeit with assemblages dominated by a few well-adapted species.

Plain Language Summary Inshore coral reefs throughout the world are highly susceptible to anthropogenic disturbance (e.g., increasing pollution and changing land use) and have declined in recent decades. Modern sea-level rises associated with global warming could theoretically increase accommodation space for corals growing on shallow reef flats. Whereas, the potential for degraded inshore coral reefs to respond to increased sea-level rise is as yet unclear. In this study, fringing reefs in Sanya Bay, a typical inshore reef system impacted by severe anthropogenic perturbations, provide a case study of disturbed inshore reefs response modern sea-level rise. With ecological surveys, coral demographic and age-frequency analyses, and high-precision U-Th dating, we provide evidence of a recent switch on of reef growth over the past 50 years in response to rising sea levels that is unprecedented since the mid-Holocene. The unique life history strategy of the dominant coral taxa (free-living *Porites*) driving this partial recovery allows them to overcome highly turbid and eutrophic environmental conditions that have previously been considered adverse to recovery through sexual recruitment. Our results provide novel insight into the response of marginal habitats to sea-level rise, and a glimpse into a potential future condition, or new state, of heavily disturbed Indo-Pacific coral reefs.

1. Introduction

Coral reefs are extremely valuable ecosystems, due to their high biodiversity and the many goods and services they provide, but they are highly vulnerable to natural and anthropogenic perturbations. Threats to coral reefs range from regional (e.g., overfishing, destructive fishing, mining, dredging, and pollution) to global scale (e.g., climatic warming and ocean acidification). Coral bleaching due to ocean-warming (Hughes et al., 2018) has impacted pristine, oceanic coral reefs throughout the Indo-Pacific Ocean, with ocean acidification causing additional stress (Pandolfi et al., 2011). For coral reefs in coastal areas, especially near developing countries such as the northern South China Sea (NSCS), acute and chronic damages from human activities are the major drivers of local reef deterioration (Hughes et al., 2012). The current status apparently

indicates a gloomy future for those inshore reefs (e.g., Hoegh-Guldberg et al., 2007; Hughes, 1994; Hughes et al., 2012).

From a geological perspective, modern fringing reefs in the Indo-Pacific region mainly formed relatively recently, in the early Holocene (~10,000–7,000 years BP; BP means *before 1950 CE*) and reached sea level at ~7,000–6,000 years BP (e.g., Kennedy & Woodroffe, 2002; Montaggioni, 2005). Since then, reef flats have existed in a largely senescent state, with no space to accommodate vertical growth (e.g., Leonard et al., 2013; Smithers et al., 2006). As reef growth approaches the sea-level surface, increasingly intense solar radiation, intermittent aerial exposure, and frequent resuspension of fine sediments create an upper limit for reef growth; *accommodation space* refers to the vertical zone below that limit that is available for reef growth. However, modern sea-level rise associated with global warming is projected to change the dynamics of reef flat environments through an increase in accommodation space for coral growth. Evidence from Pacific coral reefs in clear-water environments such as Heron Island, Australia (Scopéltis et al., 2011), Solomon Islands (Saunders et al., 2016), and Palau (van Woesik et al., 2015) indicates that rising sea levels can promote coral colonization on reef flats. However, the potential for degraded inshore coral reefs to respond to increased sea-level rise is still unclear. The colonization and growth of inshore reef flats is critically important, because modern fringing reefs play an important role as protective barriers against storms and coastal erosion in many heavily populated and developing regions (e.g., Alegria-Arzaburu et al., 2013; Reguero et al., 2018) and are more accessible for tourism use.

In this study, we use ecological surveys, annual growth band analysis, and coral demographic analyses, and high-precision U-Th dating, to explore the response of a reef flat to recent sea-level rise in the NSCS. The NSCS is one of the *highly impacted regions* of the world (Halpern et al., 2008), where human activities have degraded inshore coral reefs and nonreefal coral communities over decades prior to recent climate change impacts (Hughes et al., 2012). We provide evidence that marginal inshore reefs are responding to increasing sea-level rise through colonization of the reef flat by populations of free-living *Porites compressa* corals. Importantly, recolonization is occurring not through settlement of larvae from ordinary sessile corals, but through the unique life-history strategy of mobile, free-living corals. The regeneration of previously dormant reef flats highlights the importance of understanding coral adaptations and survival strategies under local human-induced disturbances and large-scale sea-level rises and provides insight into resilience of inshore coral reefs and their possible futures.

2. Materials and Methods

2.1. Study Site

Sanya Bay is adjacent to Sanya City in southern Hainan Province/Island, NSCS (Figures 1a and 1b). Sanya City has a resident population of ~700,000, but experiences an annual influx of more than 16,000,000 tourists each year (McCook et al., 2017). Sanya River (Figure 1b), with an annual flow of $2.11 \times 10^9 \text{ m}^3$ (Huang et al., 2003), continuously inputs freshwater, sediments, and urban, industrial, and agricultural pollutants into Sanya Bay. Coupled with marine aquaculture and tourism industry development, the water environment in Sanya Bay has experienced substantial eutrophication and increases in turbidity over recent decades (Hughes et al., 2012; Zhao et al., 2012). As a consequence, coral reefs in Sanya Bay have deteriorated dramatically over the past 50 years, with coral cover declining from ~80% in the 1960s to ~12% at present and at least one third of coral species now regionally extinct (Zhao et al., 2012). Destructive fishing and extensive coastal development (e.g., expansion of Sanya port, new hotels, artificial islands) have further added to the decline (Fiege et al., 1994; Hughes et al., 2012; Zhang et al., 2006; Zhao et al., 2012). Chronic rates of sedimentation are exceptionally high, sometimes exceeding $20 \text{ mg}\cdot\text{cm}^{-2}\cdot\text{day}^{-1}$, and resuspension of fine silt-clay sediments affect recovery and survival of coral assemblages (Li, Huang, Lian, Liu, et al., 2013). Increased turbidity associated with high resuspension during the rainy and typhoon seasons (Li, Huang, Lian, Liu, et al., 2013) and extreme sedimentation events from dredging (Li, Huang, Lian, Yang, et al., 2013) create an adverse environment for coral survival.

2.2. Field Sampling

Surveys on the Sanya Bay reef flat were conducted in May 2016 and June 2017 at low tides, within an ~800 × 200 m² study area (Zone A, Figure 1c). Total coral cover was determined by surveying three 100-m-

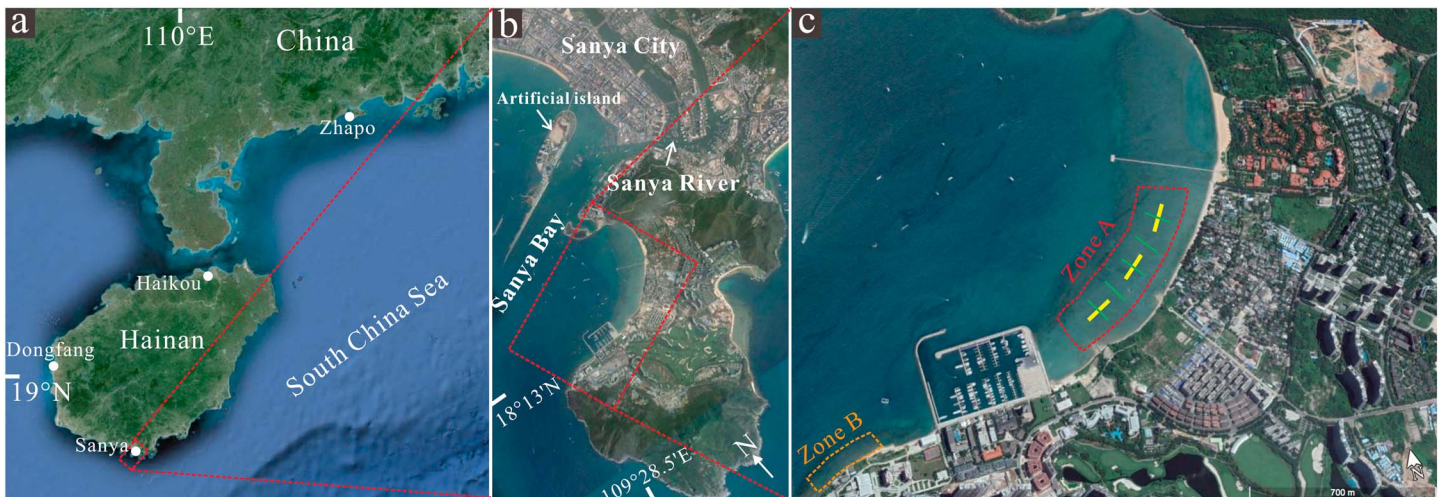


Figure 1. Maps of the study site. (a) Hainan Island/Province and the northern South China Sea; inset (b) Sanya Bay, Sanya River, and Sanya City; and inset (c) reef flat study sites (zones A and B). Parallel yellow lines ($n = 3$) in Zone A represent the locations of line intercept transects for living coral cover measurements, and perpendicular green lines ($n = 5$) in Zone A represent the transects for *Porites* colony size measurements. Surface U-Th dates of Holocene reef flats were collected in Zones A and B to determine the accretionary history of the fringing reef in Sanya Bay. All base maps here were downloaded from Google Earth (Google Company).

long line intercept transects parallel to the shore (Figure 1c). The maximum width of *Porites* colonies (>5 cm in size, $n = 166$ total) were measured along five ~ 100 -m-long transects placed perpendicular to the shore (Figure 1c).

In Zone A (Figure 1c), one slice, ~ 8 mm-thick, was cut from four, individual medium-sized live *Porites* colonies in situ for species identification and estimates of skeletal extension rates. To determine the Holocene accretionary history and surface age of corals on the reef flat, 11 fossil *Acropora* branches (Figure 2c) were randomly collected throughout Zone A, and a small fragment (~ 200 g) was collected from each of 12 fossil microatoll *Porites* in Zone B as indicators of historical sea-level maxima (Figure 2d).

2.3. X-Ray Photography and Species Identification

In the lab, the four coral slices were immersed in 10% H_2O_2 for 24 hr, then cleaned with fresh water in an ultrasonic cleaner (10 min, three times) and then dried at $50^\circ C$ in an oven. The coral slices were X-rayed and the positive prints revealed the annual density pattern (Figure 3). Microstructures of the *Porites* corallite were examined with a stereomicroscope and used as the basis for species identification (Veron, 2000; Zou, 2001). The annual growth rate of each coral slice was measured directly on the X-ray photos according to the width of the annual bandings (Figure 3). The mean growth rate for the *Porites* species was calculated based on the four slices.

2.4. U-Th Dating for Fossil Corals

Surfaces of all fossil *Acropora* branches and *Porites* fragments were polished and the fresh skeletons were crushed into ~ 1 -mm-diameter grains. Grain samples from each coral (~ 150 mg) were cleaned and weighed at the Radiogenic Isotope Facility, School of Earth and Environmental Sciences, University of Queensland. U-Th isotopic ratio measurements were performed on a multicollector inductively coupled plasma mass spectrometer following the analytical protocol described by Clark, Roff, et al. (2014) and Clark, Zhao, et al. (2014).

2.5. Sea-Level Data

Annual mean sea-level data (Figure 4) from Dongfang (1970–2016), Haikou (1975–2016), and Zhapo (1959–2016) monitoring stations (Figure 1a) were obtained from the Permanent Service for Mean Sea Level (<http://www.psmsl.org/>). To compare local sea-level rise with global sea-level rise, reconstructed global mean sea level (Church & White, 2011) was obtained from CSIRO (http://www.cmar.csiro.au/sealevel/sl_data_cmar.html). Sea-level anomalies were determined as deviations from 1993 to 2011 baselines for each time series.

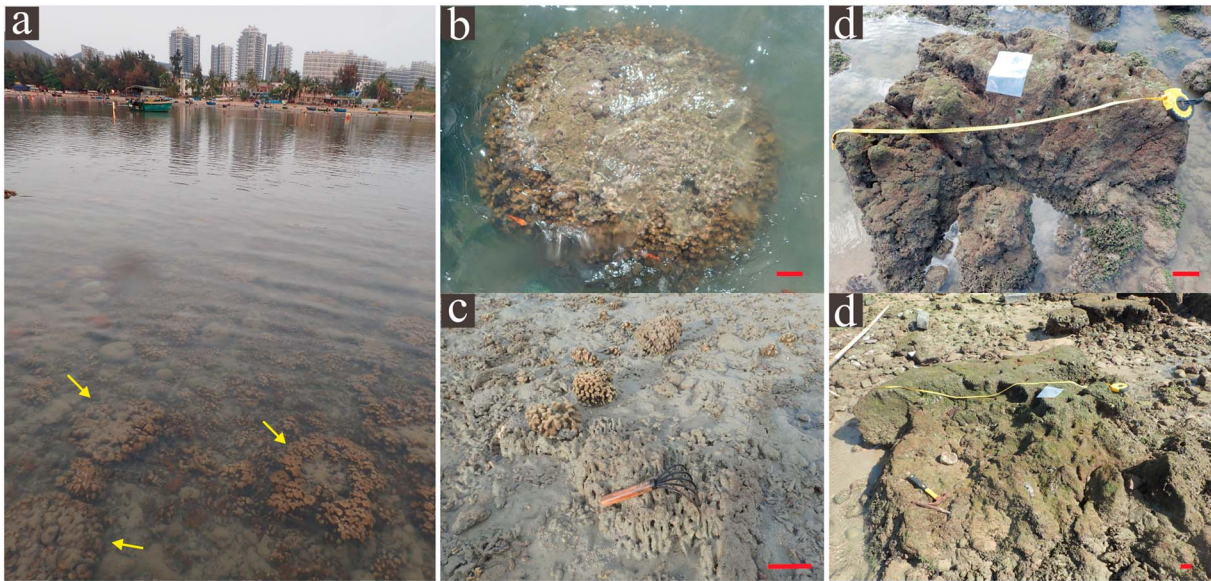


Figure 2. Photos of living and fossil corals in our study area. (a) Dense live *Porites* coral assemblages on the reef flat (Zone A). Aerial exposure of those *Porites* occurs at low spring tides. Some microatolls, that is, coral colonies with living, steep-sided perimeters but dead top surfaces, on the reef flat are indicated by yellow arrows. (b) The biggest live *Porites* colony (a microatoll) in Zone A, with a maximum width of ~120 cm. (c) Fossil *Acropora* branches adjacent to living *Porites* corals. (d) Representative in situ photos of the fossil *Porites* microatolls in Zone B. Red bars in photos (b), (c), and (d) represent 10 cm as scale.

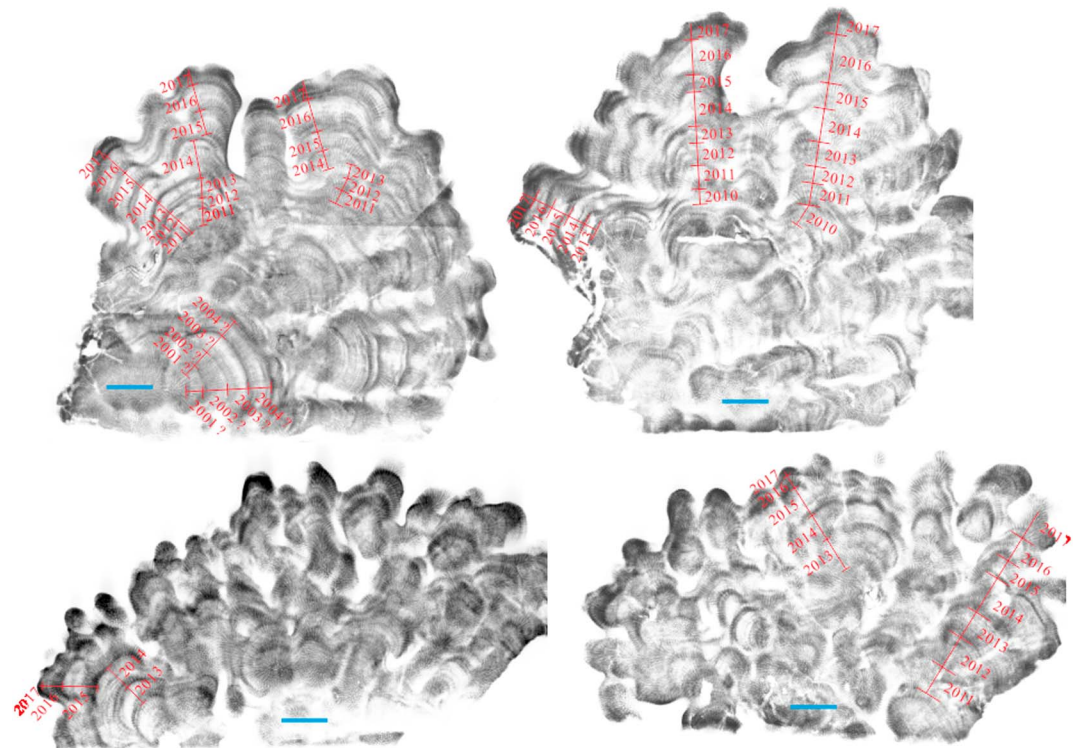


Figure 3. X-radiography positives of four *Porites* slices collected from the reef flat in Sanya Bay. Dark bands represent the high density portion of the coral skeletons, while light bands represent the low density portion. A couplet of high density and low density bands represent a single year of growth (blue bars = 2 cm scale). Transects for measurements of annual banding are indicated by the red lines, with banding marked by years.

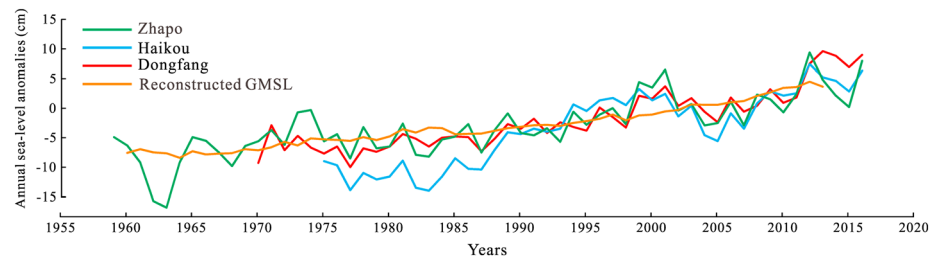


Figure 4. Anomalies of annual mean sea-level records from Dongfang, Haikou, and Zhapo for the northern South China Sea, and reconstructed GMSL data for the global mean sea level. GMSL = global mean sea level.

3. Results

3.1. U-Th Dating of the Holocene Reef Flat

The U-Th dating results (Table 1) indicate that surface fossil *Acropora* and *Porites* corals on the reef flat ceased growing in the mid-Holocene. U-Th ages obtained from fossil *Porites* heads in Zone B were $\sim 6,400$ years BP, while fossil *Acropora* branches in Zone A were younger (from 5,802 to 5,341 years BP). These ages indicate that the reef flat ceased growing following the end of the mid-Holocene high sea level, which was $\sim 1\text{--}2$ m above modern sea level in the western Pacific from $\sim 7,000$ to $\sim 5,500$ years BP (e.g., Leonard et al., 2016; Meltzner et al., 2017; Yu et al., 2009).

3.2. Modern Sea-Level Rise

Analysis of local sea-level anomalies from Dongfang (1970–2016) and Haikou (1975–2016) are consistent with the longer trend of increasing sea levels from the Zhapo monitoring station between 1959 and 2016 (Figure 4). Local sea-level rise was 16.2 ± 0.6 cm over the past 30 years (1987–2016), consistent with the trend of increasing global mean sea level over recent decades (Figure 4). This rise has generated increased accommodation space on these reef flat habitats.

3.3. Species Identification and Skeletal Growth Rate

Based upon morphology and corallite microstructures, the dominant species of *Porites* coral on the reef flat was identified as *P. compressa* (Dana, 1846). X-ray analysis of skeletal density banding patterns (Figure 3) indicates a mean growth rate of 10.8 ± 1.7 mm/year (mean \pm SD; $n = 58$).

3.4. Ecology of *Porites* Assemblages

Living coral cover along the three line-intercept transects on the reef flat (Zone A) averages $19.9 \pm 1.5\%$. *P. compressa* is the dominant species, averaging $13.9 \pm 1.3\%$ cover (Figure 2a). The remaining coral species include branching *Montipora digitata*, massive *Favites* spp., and massive *Platygyra* sp., all of which are growing attached to hard substrate. In contrast, the dominant *P. compressa* forms free-living colonies that grow unattached on muddy substrates, with a subspheroidal submassive growth form (Figure 5). *P. compressa* colonies range in size from ~ 5 to 120 cm. Assuming a direct relationship between size and age for free-living *P. compressa* colonies, colonies range between 2 and 56 years old, with the majority (86%) of colonies less than 30 years of age (Figure 6).

Smaller mobile colonies of *P. compressa* ($< \sim 50$ cm in diameter) remain submerged during temporary aerial exposure at low spring tides (Figure 2c), while the upper surface of larger colonies ($> \sim 50$ cm in diameter) are emergent at low tide, resulting in the formation of permanent microatolls (Figure 2b).

The unique morphology of the *P. compressa* colonies changes through at least four different growth phases. Small free-living colonies, or *coralliths*, with diameters under ~ 10 cm, are completely covered by living tissue, although the upward parts appear gray (Figures 5a and 5b). Juvenile colonies have a radial, subspheroidal morphology, with branches occurring on either the top or bottom (Figure 5a). Sections of small-free living colonies revealed no solid material other than coral skeleton, indicating that the colonies form primarily from asexual fragmentation of existing colonies and not through settlement of larvae onto dead coral fragments. The radial, subspherical morphology implies that these fragments move and rotate in response to water motion and bioturbation. As the *P. compressa* coralliths increase in size and weight, they become less spherical and form an oblate spheroid (Figures 5b and 5c). These rotate less frequently, and when they eventually

Table 1
U-Th Dating of Fossil *Acropora* and *Porites* Corals in This Study

Sample ^a	²³⁸ U (ppm)	²³² Th (ppb)	²³⁰ Th/ ²³² Th	²³⁰ Th/ ²³⁸ U	²³⁴ U/ ²³⁸ U	Uncorrected age (ka)	Corrected age (ka)	Corrected initial ²³⁴ U/ ²³⁸ U	Age (BP) (corrected)
A-1	3.6710 ± 0.0017	19.16 ± 0.02	33.200 ± 0.081	0.057098 ± 0.000125	1.1442 ± 0.0010	5.584 ± 0.013	5.481 ± 0.024	1.1466 ± 0.0010	5414 ± 24
A-2	3.1388 ± 0.0013	9.72 ± 0.01	57.58 ± 0.16	0.058767 ± 0.000151	1.1459 ± 0.0011	5.743 ± 0.016	5.681 ± 0.020	1.1483 ± 0.0011	5613 ± 20
A-3	3.4567 ± 0.0017	2.74 ± 0.00	226.21 ± 0.60	0.059012 ± 0.000137	1.1456 ± 0.0007	5.769 ± 0.014	5.751 ± 0.015	1.1480 ± 0.0007	5683 ± 15
A-4	3.6100 ± 0.0018	5.00 ± 0.01	130.27 ± 0.36	0.059457 ± 0.000147	1.1427 ± 0.0015	5.829 ± 0.017	5.800 ± 0.018	1.1451 ± 0.0016	5732 ± 18
A-5	3.2016 ± 0.0016	33.49 ± 0.05	17.154 ± 0.050	0.059144 ± 0.000153	1.1443 ± 0.0010	5.789 ± 0.016	5.586 ± 0.044	1.14696 ± 0.0010	5818 ± 44
A-6	3.6728 ± 0.0012	22.14 ± 0.05	30.84 ± 0.15	0.061271 ± 0.000263	1.1470 ± 0.0009	5.988 ± 0.027	5.870 ± 0.036	1.1497 ± 0.0009	5802 ± 36
A-7	3.4328 ± 0.0013	8.47 ± 0.01	69.19 ± 0.21	0.056279 ± 0.000139	1.1460 ± 0.0009	5.493 ± 0.015	5.443 ± 0.018	1.1484 ± 0.0009	5375 ± 18
A-8	3.6583 ± 0.0020	5.32 ± 0.01	124.38 ± 0.44	0.059654 ± 0.000180	1.1468 ± 0.0010	5.827 ± 0.019	5.797 ± 0.020	1.1493 ± 0.0010	5729 ± 20
A-9	3.3153 ± 0.0014	8.11 ± 0.01	71.58 ± 0.20	0.057728 ± 0.000141	1.1448 ± 0.0011	5.644 ± 0.015	5.594 ± 0.018	1.1472 ± 0.0011	5527 ± 18
A-10	3.4649 ± 0.0010	5.01 ± 0.01	121.73 ± 0.39	0.057999 ± 0.000165	1.1440 ± 0.0013	5.675 ± 0.018	5.645 ± 0.019	1.1464 ± 0.0013	5577 ± 19
A-11	3.3868 ± 0.0012	4.91 ± 0.01	116.53 ± 0.41	0.055687 ± 0.000183	1.1449 ± 0.0007	5.439 ± 0.019	5.409 ± 0.020	1.1472 ± 0.0007	5341 ± 20
B-1	2.7848 ± 0.0017	13.39 ± 0.02	41.13 ± 0.11	0.065188 ± 0.000155	1.1428 ± 0.0009	6.406 ± 0.017	6.311 ± 0.025	1.1455 ± 0.0009	6243 ± 25
B-2	2.6964 ± 0.0013	5.58 ± 0.01	80.23 ± 0.24	0.064498 ± 0.000187	1.1431 ± 0.0011	6.335 ± 0.020	6.284 ± 0.022	1.1457 ± 0.0012	6217 ± 22
B-3	3.0831 ± 0.0016	107.21 ± 0.13	6.36 ± 0.02	0.072863 ± 0.000187	1.1424 ± 0.0015	7.187 ± 0.021	6.516 ± 0.135	1.1461 ± 0.0015	6448 ± 135
B-4	2.7763 ± 0.0018	11.58 ± 0.07	47.80 ± 0.46	0.065711 ± 0.000497	1.1446 ± 0.0009	6.449 ± 0.050	6.365 ± 0.053	1.1473 ± 0.0009	6298 ± 53
B-5	3.2076 ± 0.0027	45.51 ± 0.22	14.71 ± 0.12	0.068776 ± 0.000471	1.1446 ± 0.0011	6.758 ± 0.048	6.484 ± 0.073	1.1477 ± 0.0011	6416 ± 73
B-6	2.8892 ± 0.0020	21.77 ± 0.14	27.51 ± 0.26	0.068304 ± 0.000471	1.1422 ± 0.0010	6.725 ± 0.048	6.577 ± 0.056	1.1451 ± 0.0011	6510 ± 56
B-7	2.8954 ± 0.0012	39.60 ± 0.16	15.42 ± 0.11	0.069496 ± 0.000402	1.1440 ± 0.0013	6.835 ± 0.041	6.569 ± 0.067	1.1471 ± 0.0013	6502 ± 67
B-8	2.9350 ± 0.0008	50.82 ± 0.21	12.02 ± 0.08	0.068603 ± 0.000372	1.1419 ± 0.0011	6.757 ± 0.038	6.421 ± 0.077	1.1450 ± 0.0011	6354 ± 77
B-9	2.8841 ± 0.0011	12.05 ± 0.05	48.49 ± 0.31	0.066793 ± 0.000333	1.1475 ± 0.0010	6.540 ± 0.034	6.457 ± 0.038	1.1504 ± 0.0011	6389 ± 38
B-10	2.7567 ± 0.0012	27.15 ± 0.08	22.14 ± 0.13	0.071866 ± 0.000369	1.1445 ± 0.0009	7.072 ± 0.038	6.880 ± 0.054	1.1477 ± 0.0010	6812 ± 54
B-11	2.8662 ± 0.0015	5.13 ± 0.01	114.02 ± 0.61	0.067193 ± 0.000304	1.1450 ± 0.0012	6.596 ± 0.032	6.558 ± 0.032	1.1478 ± 0.0012	6490 ± 32
B-12	3.2028 ± 0.0009	60.98 ± 0.20	10.209 ± 0.053	0.064060 ± 0.000256	1.1434 ± 0.0012	6.289 ± 0.027	5.920 ± 0.078	1.1464 ± 0.0013	5853 ± 78

^a“A” represents fossil *Acropora* branches collected from Zone A; “B” represents fossil *Porites* coral heads collected from Zone B.

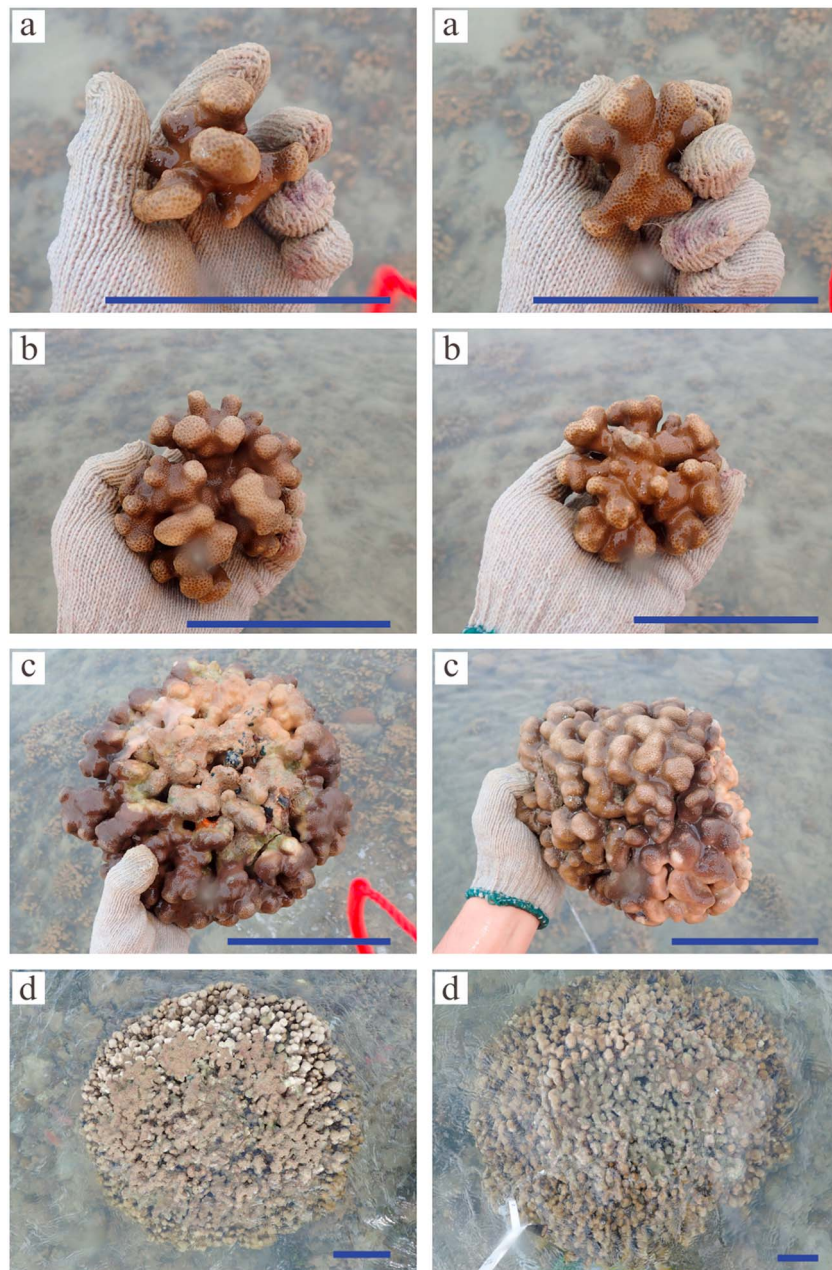


Figure 5. Four different growth phases of *P. compressa* at Sanya Bay reef flat: (a) Juvenile mobile colony (~6 cm) with a radial, submassive morphology; (b) mid-size mobile colony (~10 cm) with a near round shape; (c) larger mobile colony (~20 cm) with an oblate spheroidal shape; (d) fixed (no-longer mobile or free-living) microatolls with living coral polyps around the perimeter and dead skeleton on the exposed upper surface (blue bars = 10 cm scale).

become stationary, the downward polyps die, apparently due to food shortage and/or smothering with sediments. As their upward growth is restricted by subaerial exposure during low tides, the *Porites* coralliths eventually develop into the microatoll form, with a dead flat top and a living steep-sided perimeter (Figure 5d).

4. Discussion

During the mid-Holocene (~7,000–6,000 years BP), reef flats in Sanya Bay were well developed with abundant branching *Acropora* spp. and scattered colonies of massive *Porites* and were able to *keep up* with rising sea levels. By around 5,400 years BP, declining sea levels were constraining vertical growth on the reef flats in

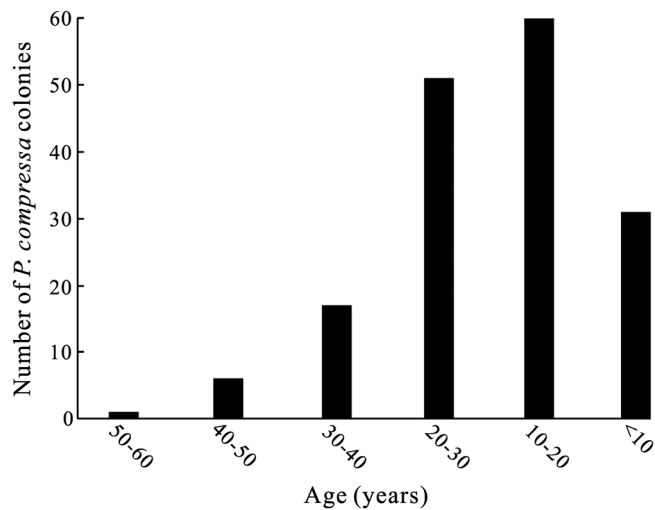


Figure 6. Age structure of *P. compressa* colonies on the reef flat.

Sanya Bay. This pattern is largely consistent with patterns of growth and decline throughout the Pacific (e.g., Leonard et al., 2013; Smithers et al., 2006). Contemporary sea-level rise (Figure 4) is releasing these constraints, providing increased space for coral assemblages in reef flat habitats. Our surveys indicate that over the past 30 years, reef flat habitats have been recolonized, reinitiating vertical growth after being dormant for millennia. Importantly, from an ecological perspective, this recolonization has occurred not through the sexual recruitment of new corals that has been critical for recovery of reefs following disturbance (e.g., Gilmour et al., 2013), but instead by asexual reproduction, forming free-living colonies that are able to survive in highly turbid environments. Asexual fragmentation and transport allow corals to bypass settlement and postrecruitment bottlenecks that typically inhibit corals exposed to high sediment levels from recovery following disturbance (see Jones et al., 2015, for a concise review). From a geological perspective, modern sea-level rise appears to be *switching on* reef growth which has been *turned off* due to limited accommodation space for over 5,000 years.

While Holocene coral assemblages were dominated by branching *Acropora*, modern assemblages are dominated primarily by *P. compressa*, along with isolated colonies of *Montipora*, *Favites*, and *Platygyra* that have recruited to the marginal reef flat environment. In deeper water on the reef flat (Zone A), modern living *P. compressa* microatolls appear to be *keeping up* with contemporary sea-level rise. Similar to fossil *Porites* microatolls formed during the mid-Holocene sea-level highstands, *P. compressa* microatolls exhibit predominantly lateral growth, with living tissues around the perimeter and dead skeleton on the exposed upper surface. Large (>~100 cm in diameter) microatolls on the reef flat are very sparse, and the majority of colonies (>80%) are small, mobile, and free-living, indicating ongoing colonization of the reef flat in recent decades in response to sea-level rise. The largest *P. compressa* microatoll surveyed was ~120 cm in diameter (Figure 2b), with an estimated age of ~56 years based on the average extension rate of *P. compressa*. The fact that modern coral assemblages on the reef flat have formed in the past ~50 years is remarkable, given the substantial eutrophication and environmental degradation that has occurred during this period (Zhao et al., 2012).

While our findings suggest that recolonization of reef flats in marginal environments can occur in response to sea-level rise, the high rates of sedimentation and eutrophication of surrounding coastal waters have resulted in a low diversity habitat, with only four genera and five species represented in our transect surveys. This contrasts with the adjacent diverse reef slope habitats, where 69 coral species from 24 genera are present (Zhao et al., 2012). Corals on the reef flat are growing in a shallow, muddy, eutrophic, and turbid inshore environment, widely considered to be marginal habitat and unfavorable for sustained coral growth. Sensitive taxa such as *Acropora* spp. that were historically dominant in the Holocene and occur in adjacent reef slope habitats (Zhao et al., 2012) are likely absent due to the effects of adverse environmental conditions on settlement and recruitment. High rates of sedimentation and low light levels negatively affect coral survival rates (Rogers, 1990). The combined effects of anthropogenic sedimentation and nutrient enrichment can severely inhibit coral recruitment and settlement, slow coral recovery, reduce resilience, and eventually induce declines in coral coverage and species richness (Abelson et al., 2005; Birrell et al., 2005; Naumann et al., 2015; Nava & Tamírez-Herrera, 2012; Wielgus et al., 2003; Yeemin et al., 2013).

In Sanya Bay, the apparent regeneration of coral reef flats by *P. compressa* and a few other species suggests that acclimatization and recovery are strongly taxon dependent. Similar cases have been noted on other inshore reefs, where distinctive community assemblages, with relatively high live coral cover, develop in suboptimum conditions (e.g., suboptimal salinity, destructive fishing, high turbidity, and eutrophication), due to the survival and successful reproduction of distinctive *tolerant taxa* or even a single tolerant species. This results in coral reefs dominated by a small number of tolerant coral species (e.g., Bauman et al., 2015; Brown et al., 2012; Guest et al., 2016; Lirman & Manzello, 2009; Sawall et al., 2013). Surveys of reef slopes in Sanya Bay have found that *P. compressa* is either uncommon or absent (Zhao et al., 2012), indicating that marginal environments may represent a niche space for remarkably stress-tolerant taxa. Additionally, the radial,

subspherical morphology of smaller colonies allows them to colonize the reef flat through water motion and bioturbation (Capel et al., 2012; Tortolero-Langarica et al., 2016). The biggest benefit of the strategy is probably the ability of juvenile colonies to survive and continue growth without burial by sediments. Between rotations, water movement through the surface layer of sediments might provide enough flushing to ensure the downward polyps remain alive (Scoffin et al., 1985).

On a local scale, while the reef flat environment at Sanya Bay is adverse to coral survival, several factors promote the persistence of the newly recolonized coral assemblages. High turbidity caused by sediments and phytoplankton blooms may further reduce light penetration and protect corals from intense solar radiation during summer, which could reduce the incidence of coral bleaching and mortality in the shallow reef-flat environment (Cacciapaglia & van Woerik, 2016). Increased levels of particulate organic matter and other components in sediments may provide an alternative source of energy for corals *P. compressa* (Anthony, 2006; Fabricius, 2005; Sofonia & Anthony, 2008). In the future, the relatively low levels of destructive fishing on the reef flat compared to reef slope environments may offer emerging assemblages protection from additional human disturbances.

On a global scale, sea-level rise of up to 0.4–0.8 m by 2100 has been predicted by the IPCC (2014). If settlement of the Sanya Bay reef flat by free-living corals persists into the future, our results suggest that sea-level rise can promote vertical and lateral growth of presently constrained coral communities in marginal, inshore reef-flat environments. Therefore, inshore coral reefs in highly degraded environments (like Sanya Bay) may change species assemblages, but not disappear entirely. Small numbers of species with high potential for adaptation to disturbance will hold important roles in local coral reef recovery. From a palaeo-ecological, evolutionary perspective, these results are broadly consistent with the hypothesis proposing the evolution of reef-building scleractinian corals in turbid environments (Potts & Jacobs, 2000). The persistence of such turbid inshore habitats through geological time may have promoted ecological and evolutionary continuity, providing a consistent refugia for corals during nonreef building periods (Potts & Jacobs, 2000). Further observations of recolonization of marginal reef flats will be critical to record the diversity and life history strategies of these unique coral assemblages. Our study provides a glimpse into a potential future condition, or new state, for heavily disturbed Indo-Pacific coral reefs.

5. Conclusions

As a representative inshore reef with severe human disturbances, reef habitats in Sanya Bay became marginal and unfavorable for coral growth and have declined markedly in recent decades. During this period, however, relatively abundant populations of submassive *P. compressa* and some other species gradually started to assemble on the reef flat. Relatively fast rise in local sea level during the last ~30 years can explain a high proportion of the observed variation in age structure of *P. compressa* colonies, with overall increasing vertical accommodation space for coral colonies, promoting coral settlements on the shallow reef flat. Modern sea-level rise potentially acts to *turn on* reef growth which has been previously turned off in the Mid-Holocene (~5,400 years BP) due to constrained accommodation space with sea-level decrease. Only *P. compressa* colonies appear to have benefitted from sea-level rise and developed into assemblages with a relatively high cover percentage. This reflects the combination of their distinctive tolerance to the marginal conditions, and their growth strategy, involving progressive modification of morphology from free-living, juvenile subspheroidal colonies to a microatoll form. Our results suggest that disturbed inshore coral reefs have been changing, with a shift toward dominance by a few well-adapted species, but will not disappear entirely. With the sustaining sea-level rise in the near future, those few species will hold an important position in local reef recovery.

Conflict of interest

The authors have no conflict of interests to declare.

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