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NOTE

Age structure of massive *Porites lutea* corals at Luhuitou fringing reef (northern South China Sea) indicates recovery following severe anthropogenic disturbance

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Abstract Luhuitou fringing reef at Hainan Island (northern South China Sea) has experienced severe anthropogenic disturbance, with live coral cover declining by > 80 % since the 1960 s. To assess the size structure of *Porites lutea*, we measured the sizes of 1,857 colonies from the reef flat (0 m) and slope (2–4 m depth). Both populations were positively skewed and leptokurtic in shape, indicating a high abundance of smaller colonies (averaging 21.4 ± 2.3 cm on the flat and 31.9 ± 2.8 cm on the slope). Age structure of populations was determined through growth rates extracted from X-rays of *P. lutea* cores. The majority of colonies (> 95 %) were < 50 yr old, with 55 % of *P. lutea* on the reef flat having recruited following the establishment of a marine reserve in 1990. The abundance of younger colonies indicates significant recovery of *P. lutea* following the removal of chronic anthropogenic disturbance.

Keywords Coral · Age structure · *Porites* · Recovery · Disturbance

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Introduction

Quantifying age structures of coral populations is a useful tool for assessing the status of coral reefs (Bak and Meesters 1998, 1999; Glassom et al. 2004). Age structures can provide insights into past environmental disturbances and can provide some predictive power in assessing the recovery of coral populations. It is assumed that positively skewed frequency distribution of coral sizes implies population growth, while a negatively skewed distribution indicates a lack of recent recruitment (Bak and Meesters 1998; Meesters et al. 2001). In the Indo-Pacific, massive corals, such as *Porites* spp., have been identified as some of the most resilient corals toward natural and anthropogenic disturbances, in part due to their inherent resistance to environmental extremes (e.g., Li et al. 2011). Despite this long-lived life history strategy, sexual recruitment of *Porites* is relatively rare compared with other shorter-lived corals, making them susceptible to protracted rates of recovery following disturbance (e.g., Done 1987). As such, age structures of massive *Porites* spp. represent a potentially useful indicator of long-term ecological process of coral reefs.

Coral communities on Luhuitou fringing reef (northern South China Sea) have undergone dramatic decline in the past 50 yrs following severe anthropogenic disturbance (coral block mining and destructive fishing), with live coral cover declining from ~ 85 % in the 1960 s to ~ 12 % in 2009 (Zhao et al. 2012). Since the establishment of Sanya National Coral Reefs Nature Reserve in 1990, disturbance from destructive activities on Luhuitou fringing reef has been significantly reduced (Qiu 2013). To assess the recovery of massive corals, we quantified the age structure of massive *Porites lutea* at 6 transects along the outer reef flat (0 m) and reef slope (2–4 m) of the Nature Reserve,

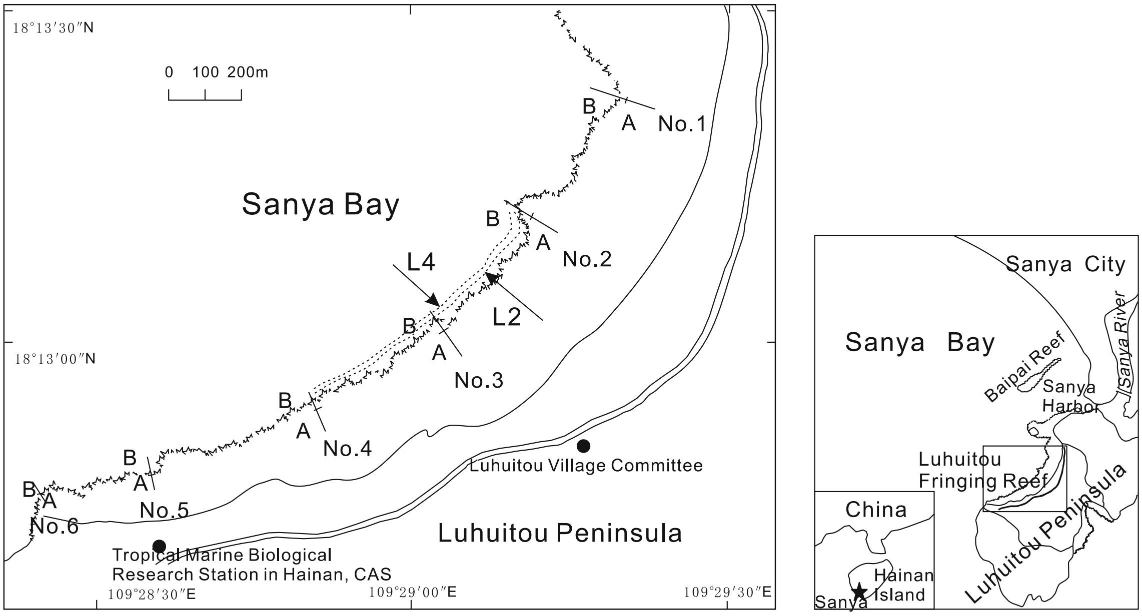


Fig. 1 Location map of Luhuitou fringing reef in Sanya Bay (Hainan Island, China) and transect locations in 2006 (*straight lines*, transects No. 1–6, *A* reef flat, *B* reef slope) and 2007 (*dotted lines*, L2 = 2 m, L4 = 4 m)

and calculated their ages based upon the measurements of growth rates extracted from *P. lutea* density bands. Our results indicate a relatively young and growing population of *P. lutea* colonies following removal of multiple chronic anthropogenic stresses and provide insight into the long-term trajectory of Luhuitou Reef.

Methods

Luhuitou Reef ($\sim$ 3 km long and $\sim$ 250–500 m wide) is situated adjacent to the Sanya urban area along the southern coast of Hainan Island (Fig. 1). Luhuitou Reef has been zoned within the Sanya National Coral Reef Natural Reserve since 1990 (Fig. 1). Field surveys were conducted during expeditions in 2006 and 2007.

Field surveys

To quantify spatial variability in the age structure at Luhuitou fringing reef, six parallel belt transects (100 m length $\times$ 1 m width) were sampled at intervals (200–500 m apart) on the reef flat (0 m depth relative to the mean sea level) and reef slope (between 2 and 4 m depth) in 2006. Two additional belt transects (1,000 m length $\times$ 1 m width) were surveyed parallel to the reef slope in 2007 at 2 and 4 m depth.

Colonies of massive *P. lutea* were counted within transects, and maximum length (*Lmax*), maximum width (*Wmax*), and maximum height (*Hmax*) were recorded using a measuring tape. Significant differences between distribution parameters (mean age, skewness, and kurtosis) were tested using a *t* test paired by transect (R, Stats package, R Core Team 2013), and a null model approach (Gotelli 2001) as follows. To construct our null model, for each of the six transects from the reef flat and reef slope, size frequency distributions (with the same number of colonies and size range) were generated at random using the “randi” function in Matlab (R2012a, Mathworks, Natick, MA, USA). Skewness values were calculated for each simulated transect, and the average skewness across transects was calculated for each depth (reef flat and reef slope). This approach was repeated for 1,000 simulations, and the percentage of simulations that showed a skewness value equal (or larger) than the actual values was quantified.

Age structure of populations

To quantify the growth rates of corals, nine cores were extracted from individual colonies of massive *P. lutea* ($n = 9$) using hydraulic drilling equipment. Following collection, cores were rinsed with freshwater then sectioned using a water-lubricated diamond-bit masonry saw to obtain coral slabs approximately 8 mm. The core slabs were dried and X-rayed to reveal their annual density bands. Linear growth rates were measured based on the X-ray pictures using CoralXDS (Helmle et al. 2002) following the major growth axis. Differences in linear growth rates among years (between cores) were tested using a linear mixed-effects model (year $\sim$ growth, R, nlme package, Pinheiro et al. 2013), with core as a random factor. Age structure of *P. lutea* colonies was calculated using the following formula: Age = (L_{max} + W_{max} + H_{max})/3LGR, where LGR is the mean linear growth rate determined from the *P. lutea* cores. Data of *P. lutea size* from the 2006 reef flat (0 m depth) and 2007 belt transects (2 and 4 m depth) were used to determine the age structure of *P. lutea* on the reef slope. Colonies were then assigned to decadal age categories (0–10, 11–20, 21–30, 31–40, 41–50, 51–60, 61–70, 71–80, > 80 yrs).

Results and discussion

In total, 1,857 colonies of *P. lutea* were measured across Luhuitou Reef. The overall size structure of *P. lutea* on the reef flat and reef slope (Fig. 2) was positively skewed and leptokurtic in shape, indicating a high abundance of smaller colonies. Significantly, higher densities of *P. lutea* were recorded on the reef flat (0.66 ± 0.14 colonies per m^2) than that of the reef slope (0.16 ± 0.02 colonies per m^2, paired *t* test, $t = 3.995$, $p < 0.05$). The mean size of *P. lutea* was significantly larger on the reef slope (31.9 ± 2.8 cm) than the reef flat (21.4 ± 2.3 cm, paired *t* test, $t_{10} = 2.894$, $p < 0.05$). Colony size ranged from 7 to 93 cm on the reef slope and 1–87 cm on the reef flat, indicating that surveys captured both juvenile recruits and small adults of *P. lutea*. Despite differences in size and colony density, no significant differences were observed in skewness between populations of *P. lutea* on the reef slope (1.12 ± 0.4) and reef flat (0.84 ± 0.2, paired *t* test, $t = 0.663$, $p > 0.5$) or kurtosis between populations of *P. lutea* on the reef slope (0.69 ± 0.6) and reef flat (2.05 ± 1.2, paired *t* test, $t = 1.017$, $p > 0.1$), indicating greater abundances of younger colonies at both depths. Of 1,000 null model simulations of size frequency distributions, none had skewness values similar or higher than actual observed data (average skewness values of −0.01 ± 0.1 for the reef slope and 0.01 ± 0.2 for the reef flat). Collectively, these results indicate a relatively young and growing population of isolated *P. lutea* colonies following extensive disturbance in the past 50 yrs and indicate a rapid recruitment rate of *P. lutea*.

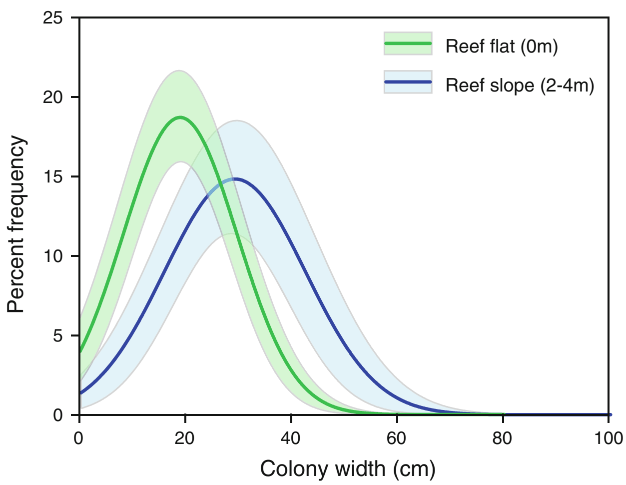


Fig. 2 Size–frequency distributions of *Porites lutea* from the reef flat (0 m) and reef slope (2–4 m depth) ± standard error (normal distributions)

In long-lived clonal organisms such as corals, the relationship between size and age is often decoupled, largely due to demographic traits such as variable growth rates, partial mortality, and colony fusion (Hughes 1984). During surveys, we were able to identify colonies of *P. lutea* as largely isolated and individual, with minimal rates of partial mortality. Growth rates of *P. lutea* ranged between

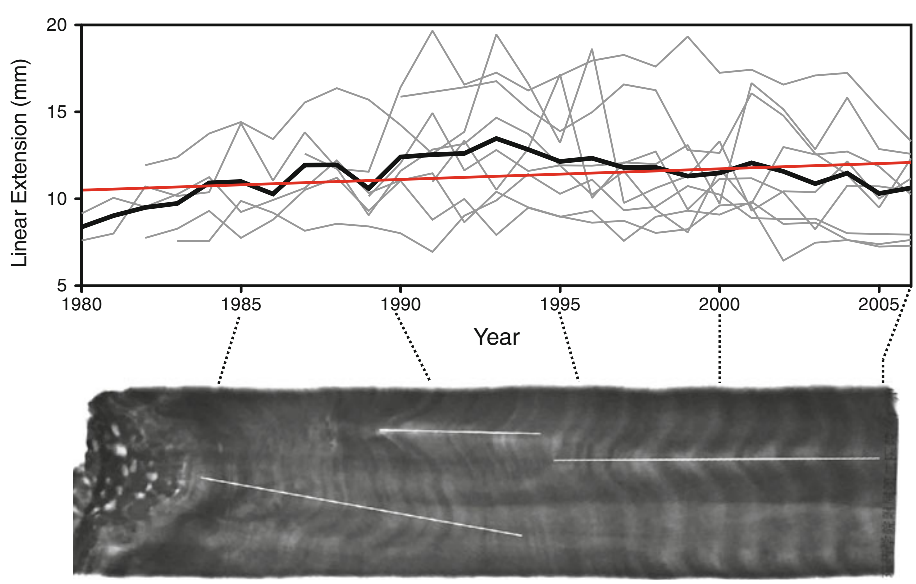


Fig. 3 Growth rates (linear extension) of nine massive *Porites lutea* colonies (*gray lines*), average linear extension (*black line*), linear regression of growth rates between 1980 and 2006 (*red line*), and X-radiograph negative of high/low-density bands

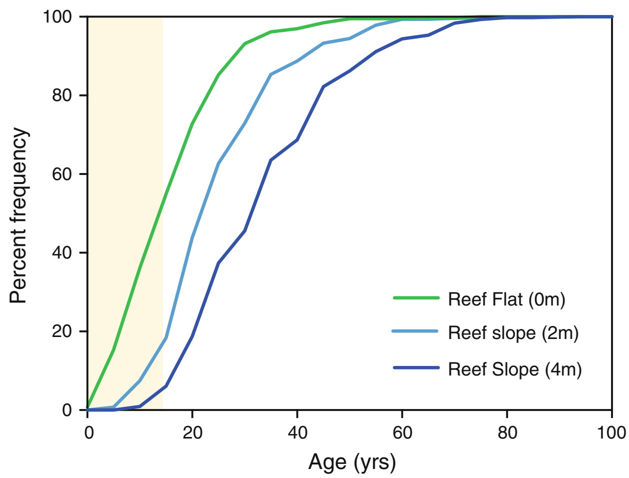
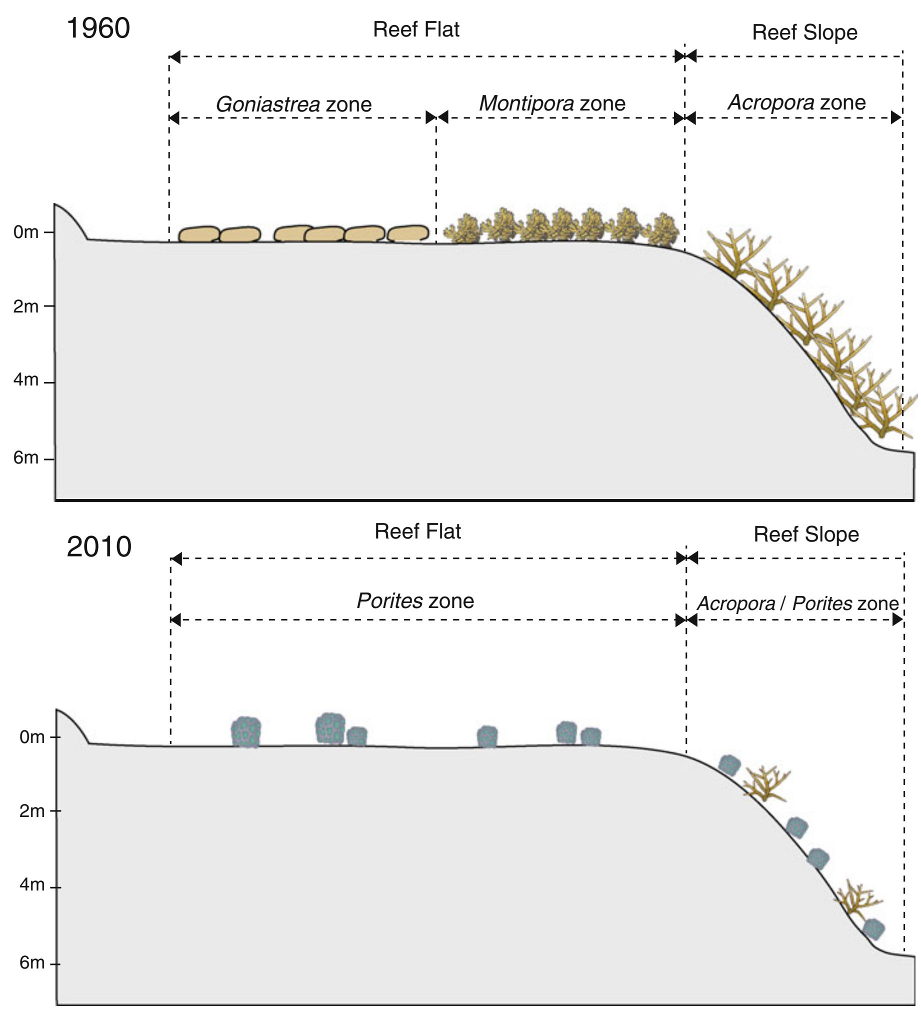


Fig. 4 Relative frequency distribution (cumulative) of *Porites lutea* ages on the reef flat (0 m depth) and reef slope (2 and 4 m depth). *Shaded region* (< 17 yr) represents the proportion of *Porites* that are younger than the initiation of the Sanya National Coral Reef Natural Reserve in 1990

9.0 ± 0.2 and 16.3 ± 0.5 mm^{-1} yr^{-1} (Fig. 3), and no significant difference in growth rates between years was observed among cores ($t = -1.16$, df $= 189$, $p > 0.1$). To constrain a size–age relationship of *P. lutea* colonies, we used the average growth rate from all nine cores between 1980 and 2006 (11.3 ± 0.2 mm^{-1} yr^{-1}), resulting in an average colony age of 25.70 ± 0.28 yr and a maximum age of 81 yrs. In total, 95.4 % of colonies were younger than 50 yrs old, indicating that Luhuitou fringing reef differs from unimpacted Indo-Pacific reefs that are typically dominated by large, well-established colonies of massive *Porites* (e.g., Kenyon et al. 2008). Populations of *P. lutea* on the reef flat were younger than either reef slope depth (Fig. 4), with 78.9 % of all colonies younger than 25 yrs, compared with 51.2 % at 2 m and 22.7 % at 4 m depth (Fig. 4).

The dominance of coral population by small or young colonies (i.e., positive skewness) is a common response of coral populations to environmental disturbance (Fong and

Fig. 5 Changes in community structure at Luhuitou fringing reef from 1960 to 2010



Glynn 1998; Done 1999; Hughes and Tanner 2000) and is indicative of a reef in an earlier successional stage following disturbance (Done 1999). In the case of Luhuitou fringing reef, the population structure is indicative of a reef in an earlier successional stage following a history of severe anthropogenic disturbance (Zhao et al. 2012). In the 1960 s, three well-defined zones were apparent (Fig. 5): a *Goniastrea aspera* zone (inner reef flat) and *Montipora digitata* zone (outer reef flat), and an *Acropora* zone (reef slope). In the present degraded state, Luhuitou fringing reef is comparatively barren, with colonies of *P. lutea* replacing the former *Goniastrea* and *Montipora* reef flat zones. Our results indicate that < 1.5 % of *P. lutea* colonies recorded on the reef flat (0 m) date beyond 1960, indicating a shift toward a novel community assemblage. On the reef slope, < 6.7 % of *P. lutea* colonies at 2 m and < 17.8 % of *P. lutea* at 4 m established prior to 1960 indicating an ongoing shift to *P. lutea* dominance on the reef slope coinciding with previously recorded severe declines in *Acropora* assemblages (Zhao et al. 2012). Despite generally low rates of recruitment in *Porites* (e.g., Done 1987), these results suggest that when other faster-growing coral competitors (i.e., *Acropora*) are removed, recruitment success of *P. lutea* is higher (as indicated by the abundance of smaller size classes our surveys).

It is generally accepted that the proportion of small or young corals is a good indicator of reef resilience (Connell 1978). The age distribution of *P. lutea* corals at Luhuitou fringing reef, with the predominance of small and young coral colonies, suggests that this reef is the undergoing signs of recovery following the establishment of the Sanya National Coral Reef Natural Reserve in 1990. Within the reserve, extractive use of marine resources (including fishing) is prohibited, ending several decades of severe disturbance through coral block mining and blast fishing (Qiu 2013). Our results indicate that 55 % of *P. lutea* on the reef flat have recruited following the establishment of the reserve, compared with 18.4 % of *P. lutea* at 2 m depth and 6.1 % at 4 m depth on the reef slope. These results are consistent with a preliminary investigation conducted 1 yr following reserve establishment, which showed that at one reef flat location, more than one-third of *P. lutea* colonies was between 1 and 3 yrs old (Yu 1995). In demographic studies of coral assemblages, percent cover of corals is often determined mainly by large colonies and is less affected by changes in the densities of young age classes (Guzner et al. 2007). Even in studies where young colonies were particularly abundant, they did not make a large contribution to total cover (Babcock 1991). While the high abundance of young *P. lutea* may not at present contribute significantly to overall percent coral cover on the reef flat due to their small overall size (Babcock 1991), continued growth of these colonies and a transition away from a positively skewed population toward a more normally distributed population may reverse the downward trend of coral cover within reserve boundaries. Considering the fourfold higher density of *P. lutea* on the reef flat compared to that of the reef slope, we expect that recovery will occur more rapidly in this environment.

The long-term declines in coral assemblages at Luhuitou Reef are largely consistent with severe declines in fringing reefs throughout the South China Sea, primarily due to coastal development, pollution, overfishing, and destructive fishing practices (Hughes et al. 2013). Despite apparent disappearance in once historically dominant coral assemblages (*Goniastrea* and *Montipora* zones on the reef flat and *Acropora* dominated reef slopes, Fig. 5), our results indicate significant recovery of the massive coral *P. lutea* following the removal of anthropogenic disturbance in reef flat and reef slope environments, and may provide insight into the recovery of coral assemblages under chronic anthropogenic disturbance.

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