



Evaluating coral reef restoration in marine protected areas using habitat structural complexity and coral communities

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Abstract Marine Protected Areas (MPAs) are widely used to protect at-risk ecosystems. This study employed a combined method to quantify the protection performance on coral reef habitats, integrating coral morphology and topographic relief in the rugosity index. In the Weizhou Island reef in the northern South China Sea, after six years of protection, the no-take areas (NTAs) hosted a greater live coral cover (11.7%) compared to the no-protection areas (NPAs, 6.9%), but had a lower rugosity (1.17)

than both the NPAs and the habitat protection areas, suggesting that while MPAs enhance coral cover, their benefits for habitat structural complexity may remain insignificant in the short term (six years). In the NTAs, the contribution of live corals to habitat complexity (28.3%) was lower than that of rubbles (34.4%). Moreover, slow-growing massive corals (e.g., *Porites lutea*), which usually have low rugosity, contributed a larger portion (up to 20%) to habitat complexity. In contrast, fast-growing, structural complex arborescent corals (e.g., *Acropora pruinosa*) had a limited contribution (2.3%). Foliose corals, which dominated the coral community also have lower rugosity (1.2~1.3) compared to massive and arborescent corals, presumably due to phenotypic plasticity in response to specific environmental conditions. This study suggests that prioritizing coral species composition, especially corals with high rugosity, is important for effective reef framework reconstruction.

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Introduction

Reef-building corals provide diverse habitats and refuges for nearly one-third of marine organisms (Fisher et al., 2015; Kerry & Bellwood, 2015;

Planes et al., 2019). In recent decades, due to climate change and human activities, a large portion of corals worldwide has bleached or died, resulting in reef collapse and unfavorable habitats (Eddy et al., 2021; Graham & Nash, 2013). To reverse coral reef degradation, resilience management and marine protected areas (MPAs) programs have been implemented as the primary reef conservation strategies around the world (Roberts et al., 2017; Hall et al., 2023; Hernández-Andreu et al., 2023). However, the effects of MPAs seem limited, as they only protect 1.7% of corals and 17.6% of fish (Mouillot et al., 2016; Selig & Bruno, 2010), or have not shown differences in fish biomass between inside and outside of protected areas (Ford et al., 2018). The protection performance of MPAs is mostly indicated by the recovery of coral biomass (e.g., live coral cover), but the limited restoration effects, e.g., on reef fishes, may be related with declines in reef habitat (Bruno et al., 2019).

Reef habitats provide a favorable environment for reef organisms, depending on the complexity of the three-dimensional reef structure that is created and maintained by living corals (Perry & Alvarez-Filip, 2019). Nevertheless, the measurement of reef complexity is often overlooked in reef monitoring studies, primarily due to the limitations of available techniques, in contrast to the more commonly assessed coral cover (Seraphim et al., 2020). The structural complexity of a reef is the basis for predicting its recovery from disturbances, and influences the biodiversity, productivity and carrying capacity of the reef habitat (Yanovski et al., 2017). When the reef structure collapses with low habitat complexity, the abundance and diversity of reef organisms were greatly reduced, such as fish (Graham & Nash, 2013; Kerry & Bellwood, 2015) and macrobenthos (Harris et al., 2018), and fishery productivity could be reduced by more than three times (Rogers et al., 2014). Conversely, a reef structure with high habitat complexity is beneficial to coral recovery, because it induces water turbulence and enhances the recruitment of coral larvae (Carlson, et al., 2024). A reef with high habitat complexity provides three times greater coastal protection compared to a reef with low habitat complexity (Yanovski & Abelson, 2019). Even if corals die, reef structures generally do not collapse at once, and they continue to provide habitats and refuges for reef organisms. Therefore, accurately

measuring habitat complexity is critical to habitat quality assessment of coral reefs.

Habitat complexity in aquatic systems is characterized by at least five traits of physical structure, e.g., spatial scales, diversity of complexity-generating physical (structural) elements, spatial arrangement of elements, sizes of elements and abundance/density of elements (Tokeshi & Arakaki, 2012). Previous studies have developed methods for assessing habitat complexity of coral reefs, for example, quantifying topographic relief and rugosity using chain intercept transects and visual assessment (Wilson et al., 2007). More complex micro-topography with higher rugosity provides more effective protection for fish and greater ecological niches available for invertebrates to settle, indicating more favorable habitats (Bozec et al., 2015; Rogers et al., 2014). Although habitat complexity and living coral cover have been used to evaluate reef functioning and quality (such as 30% coral cover for a healthy condition of the reef), substrate composition and coral community composition are often overlooked in the assessment of habitat complexity (Denis et al., 2017).

The interaction between habitat complexity and community composition is critical, as greater structural complexity across various substrate types creates a more diverse environment that supports a broader range of coral species, ultimately influencing the overall structure of the reef ecosystem. Reefs with similar topographical relief may vary in substrate compositions, e.g., with higher coral cover or higher rubble cover, thus providing different habitats for benthic organisms. Moreover, reefs with similar living coral cover may vary in topographical relief. This is because the coral community may be dominated by various coral species with different morphologies, influencing reef structural complexity, or carbonate production/erosion and net accumulation of coral reefs (Gonzalez-Barrios & Alvarez-Filip, 2018). The community composition of coral reefs impacts the reef-building processes and habitat development, depending not only on the number of coral colonies, but also on the traits of coral species (Gonzalez-Barrios & Alvarez-Filip, 2018). Specifically, diverse coral morphologies such as arborescent, massive and foliose are critical factors affecting the structural complexity of habitats (Denis et al., 2017). Even if corals recover from disturbances, corals with flat morphologies, instead of complex, three-dimensional

reef structure, may not favor the recovery of biodiversity and biomass. Therefore, a method that considers the effects of coral communities and topographic relief may help to accurately quantify the structural complexity of reef habitats. A rigorous assessment on habitat complexity could offer a useful and versatile framework for the conservation and management of ecosystems (Tokeshi & Arakaki, 2012).

The Weizhou Island reef in the northern South China Sea was selected as the case study. In this region, no-take areas (NTAs) and habitat protected areas (HPAs) have been established to reverse the declines in coral reefs as rapid growth in industries and tourism since 1990 (Wang et al., 2016; Yu et al., 2019). This study employed a combined method that integrated chain intercept transects and substrate composition, to measure rugosity of coral reefs in the NTAs, HPAs and no-protection areas (NPAs), and compared the contribution of each composition to habitat complexity, then analyzed the ecological performance of the protected areas and the possible reasons.

Materials and methods

Study area

The Weizhou Island (21°00′–21°10′N, 109°00′–109°15′E) covers an area of 25 km²

(Fig. 1a). The annual average sea surface temperature is 24.6 °C, with the highest monthly average sea surface temperature ranging from 17.3 °C to 30.4 °C (Yu et al., 2004). The average wave height around the island is 0.6 m, and the tidal range is 2.35 m. The annual average surface salinity varies from 31.4 to 33.0 psu, and the pH values range from 8.0 to 8.23 (Wang et al., 2016).

The Weizhou Island reef is mainly distributed on volcanic basement, ranging from 0.1 to 2.56 km away from the coast, in water depths of 0.5 to 6 m (He & Huang, 2019). The coral cover has dropped from 42% in 1984 to 10% in 2015, as it was threatened by rapid growth in industries and tourism since 1990 (Wang et al., 2016; Yu et al., 2019). To restore the coral reef ecosystem, a national marine park was established in the Weizhou Island in 2013 (Table 1). The NTAs are situated in the northeast part of the island, covering an area of 12.78 km², representing 40% of the reef area. Fishing and other exploitative activities are not permitted in the NTAs. The HPAs are situated in the southeast and southwest parts of the island, covering 12.34 km², representing 38.5% of the reef area. Leisure fishery and tourism are allowed in the HPAs, but commercial fishing and polluted water discharge are not permitted. The NPAs are situated outside of the national marine park.

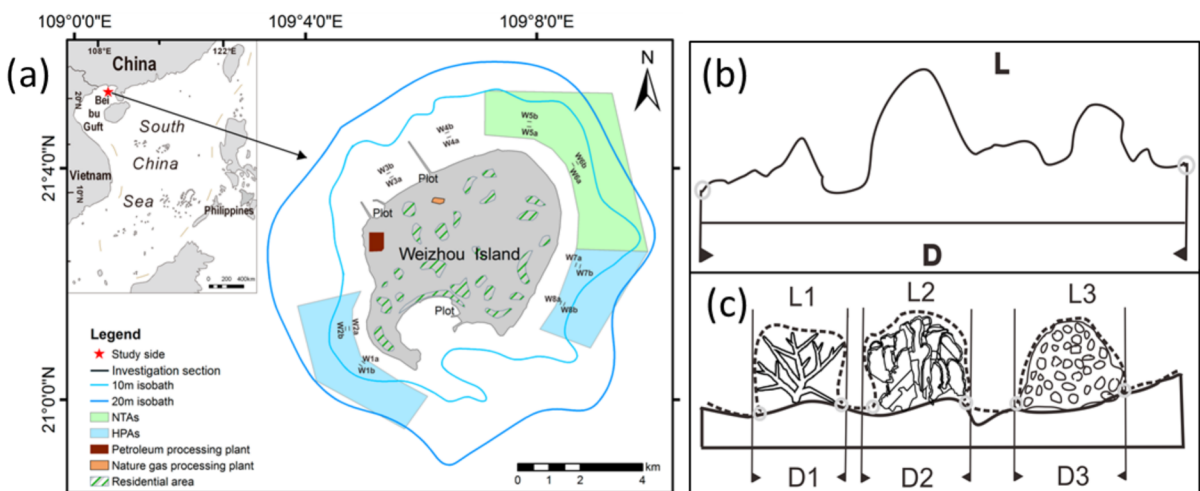


Fig. 1 Map of the study area (Weizhou Island) (a), and conceptual images for calculating the rugosity index (b and c). L is the surface contour distance, and D is the linear distance of the substrate

Table 1 Management policies for coral reefs in the Weizhou Island

Type	Management policy	Location	Area	Percentage
NTAs	Fishing and other exploitative activities are not permitted	northeast part of the island	12.78 km ²	40%
HPAs	Leisure fishery and tourism are allowed in the HPAs, but commercial fishing and polluted water discharge not permitted	southeast and southwest parts of the island	12.34 km ²	38.5%
NPAs	/	northwest parts of the island	6.87 km ²	21.5%

Table 2 Geographic information for sampling sites in the Weizhou Island

Site	Latitude and longitude	Depth (m)	region
W1a	109°05'05"E, 21°00'31"N	5.9	HPA
W1b	109°04'52"E, 21°00'37"N	7.9	HPA
W2a	109°04'48"E, 21°01'13"N	5.6	HPA
W2b	109°04'36"E, 21°01'21"N	5.9	HPA
W3a	109°05'18"E, 21°04'12"N	4.6	NPA
W3b	109°05'183"E, 21°03'57"N	8.2	NPA
W4a	109°06'31"E, 21°05'00"N	4.8	NPA
W4b	109°06'33"E, 21°04'39"N	7.4	NPA
W5a	109°07'36"E, 21°05'08"N	3.0	NTA
W5b	109°07'36"E, 21°04'46"N	6.5	NTA
W6a	109°08'40"E, 21°03'55"N	4.0	NTA
W6b	109°08'27"E, 21°03'48"N	6.4	NTA
W7a	109°08'43"E, 21°02'03"N	5.3	HPA
W7b	109°08'19"E, 21°02'09"N	6.3	HPA
W8a	109°08'20"E, 21°01'40"N	4.7	HPA
W8b	109°08'19"E, 21°01'42"N	9.1	HPA

Field investigation

Field surveys were conducted in August 2019 by using modified line intercept transects with video sampling and chain intercept transect methods (Hill & Wilkinson, 2004). Eight stations (W1–W8) were set in the southwest, northwest, northeast, and southeast of the island. Transects (50 m long) were laid at the reef flat (a: 3~5.9 m depth) and reef slope (b: 5.9~9.1 m depth) at each station (Fig. 1a and Table 2). Using 16 transects to represent reef conditions is reasonable since there were no significant differences in environmental physical variables across the three areas, including salinity, pH, *chl-a*, DIN and DIP (Huang et al., 2021a). Additionally, according to the wave observation data of the Weizhou Ocean Monitoring Station, the annual average wave height was 0.6 m, with minimal variation in wave conditions between regions (0.5~0.6 m in NTAs,

0.5~0.8 m in HPAs, 0.4~0.5 m in NPAs) (Huang et al., 2021b). An Olympus TG-3 zoom digital, waterproof camera with a wide-angle lens (1080p resolution) was positioned 20–30 cm above the measuring tape to record videos of each transect. At every 10 m interval (six measuring points), chains were laid along each line transect, following the contour of the substrate, to obtain the reef surface contour distance (Fig. 1b). A 1 m measuring rod was used as the linear distance of the chain, and photos were taken every 20 cm. A total of 576 images from 16 line transects and 96 chains were obtained.

Data analysis

The substrate composition in the coral reefs was obtained according to the relative coverages of rock (remnants of the coral reef framework created by corals in the past), rubble, sand, sponge, actinia and living coral. The coverages of these six categories were extracted from the videos by calculating the fractions of their length at each site relative to the total length of each transect. Coral species and morphology were identified with reference to "*Fauna sinica—hermatypic coral*" (Zou, 2001) and "*Corals of the world*" (Veron, 2000). The contribution of each coral species/morphology to the structural complexity was analyzed. Additionally, survey data on living coral cover in the Weizhou Island in 2008 and 2015 were used to analyze the effectiveness of coral recovery efforts (Yu et al., 2019).

The rugosity index (*RI*) was used to assess the structural complexity of habitat (Wilson et al., 2007). The scores of *RI* were calculated using the ratio of the reef surface contour distance to the linear distance (Fig. 1b), by the following formula (1).

$$RI = (\sum_{k=1}^m L_k/D)/m \quad (1)$$

where L_k is the surface contour distance at the k^{th} measuring point; D is the linear distance (1 m); m is the number of measuring points (six points). A higher score of RI indicates a more complex structure.

To quantify the differences in structural complexity among substrate types (Fig. 1c), we calculated the scores of RI for the six categories of substrate (i.e., rock, rubble, sand, sponge, actinia and living coral) and each coral species/morphology using the following formula (2).

$$RI_i = \left(\sum_{j=1}^n L_{ij} / D_{ij} \right) / n \tag{2}$$

where RI_i is the rugosity index of the specific substrate i ; L_{ij} and D_{ij} are the surface contour distance and linear distance of the specific substrate i , respectively; n is the total number of the specific substrate i .

Furthermore, we calculated the contribution of each substrate and coral species/morphology (RI_i) to the structural complexity of the habitat (RI), by using the following formula (3).

$$C_i = \left(\sum_{j=1}^n (L_{ij} - D_{ij}) / \sum_{k=1}^m (L_k - D) \right) \times 100\% \tag{3}$$

where C_i is the contribution of the substrate type i to the habitat rugosity; L_{ij} , D_{ij} , L_k , n and m are the same as formulas 1 and 2.

Linear mixed-effects models (LMMs) were performed to analyze the significant differences of RI and coral cover across three areas (fixed factors: NTAs, HPAs and NPAs), two habitats (fixed factors: reef flat and reef slope), and eight sites (random factor). The correlation between RI and coral cover was further determined by the Pearson correlation test to examine whether RI enhanced as the increase in coral cover. Variations in RI across substrate types, as well as coral morphology, were analyzed with the Kruskal–Wallis test; then, pairwise comparisons were made using Nemenyi’s all-pairs test (PMCMRplus R-package, ver. 1.9.7, <https://cran.r-project.org/web/packages/PMCMRplus/index.html>) with chi-square correction for ties. To examine the changes in substrate composition and contribution to RI across the three areas, we conducted analysis of similarities (ANOSIM) based on 999 permutations and Bray–Curtis distances (Vegan R-package, ver. 2.6–4, <https://cran.r-project.org/web/packages/vegan/index.html>). All statistical analyses were conducted in R software (ver. 4.3.0, <https://www.r-project.org/>).

Results

Mismatch between recoveries of habitat rugosity and live coral cover

The values of RI averaged $1.20 (\pm 0.01)$ and ranged from 1.15 to 1.25 at the eight stations (Fig. 2a; $df=1$, $P=0.25$). The reef slope and reef flat had similar RI values (1.20 ± 0.02 ; $F_{1, 7}=0.025$, $P=0.88$). Slightly higher RI values (1.15~1.28) occurred in the reef slope at five stations (W1, W4, W5, W6 and W7) compared to the reef flat (1.12~1.22), while slightly lower values of RI (1.13~1.26) occurred in the reef slope at the other three stations (W2, W3 and W8) compared to that of the reef flat (1.22~1.32). The low RI in both reef slope and reef flat show the marked degradation in three-dimensional structure of reef.

The coral cover averaged $15\% (\pm 3\%)$ and ranged from 5 to 32% at the eight stations (Fig. 2b; $df=1$, $P=0.42$). Only two stations (W3 and W4) had a coral cover less than 10%. Except for W5 and W8, the other six stations had relatively higher coral cover on the reef slope (7~38%) compared to the reef flat (1~25%). On average, the reef slope had a greater coral cover (18.5%), which was 1.66 times higher than that of the reef flat (11.1%) ($F_{1, 7}=4.49$, $P=0.072$). Nevertheless, the reef slope and reef flat had similar values of RI . Regression analysis showed that there was no statistically significant relationship ($R^2=0.015$, $df=14$, $P=0.65$) between the RI and the living coral cover (Fig. 2c). The results indicated that while the MPAs improved coral cover, the effects on habitat rugosity remained insignificant. This mismatch may link to the substrate or coral composition that needs a long period to restore.

Habitat rugosity and live coral cover in different regions of the MPAs

The values of RI varied slightly in the NTAs (1.17 ± 0.02), HPAs (1.21 ± 0.02) and NPAs (1.21 ± 0.03) (Fig. 3a; $F_{2, 5}=0.36$, $P=0.72$). The RI inside the MPAs was lower than that of outside, indicating a limited efficiency of habitat recovery in the MPAs. The values of RI varied among the six substrate types, i.e., living corals (1.24 ± 0.17), rocks (1.32 ± 0.05), rubble (1.09 ± 0.01), sand (1.04 ± 0.01), sponges (1.11 ± 0.02) and actinia (1.11 ± 0.01)

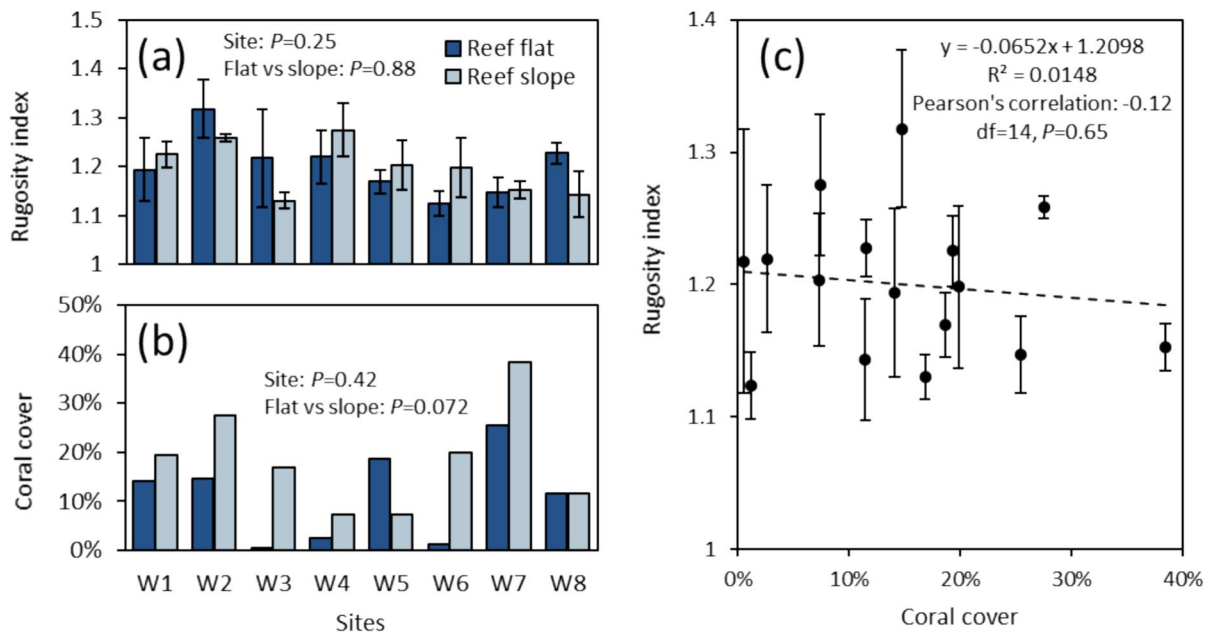


Fig. 2 Rugosity index (a) and coral cover (b) in the reef flat and reef slope across eight study sites. Correlation between the rugosity index and coral cover of the reef habitat (c). Mean and standard error (SE) are shown

(Fig. 3b; Kruskal–Wallis $\chi^2 = 24.71$, $df = 5$, $P < 0.001$).

Between 2008 and 2015, coral cover decreased from 17.5% to 4% in the NPAs, from 12.5% to 5% in the HPAs, and from 25 to 8% in the NTAs (Fig. 3c). Between 2015 and 2019, coral cover in the HPAs and NTAs increased to 20.3% and 11.7%, respectively. Whereas the coral cover continued to decrease to 6.9% in the NPAs. In 2019, the NTAs had a higher coral cover but a lower *RI* than the NPAs. It seemed that the MPAs efficiently mitigated the declines in coral biomass, but habitat complexity still failed to restore under the protection.

The analysis of substrate composition at the eight stations showed that live corals were the primary benthic organisms in reef habitats ($14.8\% \pm 2.6\%$ cover, ranging from 0.6% to 38.5%), followed by sponges ($1.7\% \pm 0.35\%$ cover, ranging from 0 to 5.02%) and actinia ($1.7\% \pm 1.42\%$ cover, ranging from 0 to 22.7%). Non-organic substrates and rocks that are beneficial for coral settlement and recruitment, accounted for $34.3\% \pm 5.3\%$ cover, ranging from 0 to 68.6%. Rubble covered $34\% \pm 6.5\%$, with a range of 5.22% to 88.78%. Sand, which inhibit coral growth, covered $13.47\% \pm 3.26\%$, with a range of 0 to 44.7%. The difference in substrate composition across the

three areas was statistically significant ($R = 0.28$, $P = 0.026$).

The substrate types, i.e., living corals, sponges, actinia, rocks, rubble and sand, respectively, contributed to 33.5%, 1.5%, 1.6%, 44.2%, 17.7% and 1.5% of *RI*. In the NTAs, the six substrate types had a cover of 11.7%, 1.7%, 6.7%, 11.4%, 61.9% and 6.5% (Fig. 3d), respectively, and contributed to 28.3%, 0%, 4.8%, 31.3%, 34.4% and 1.2% of *RI* (Fig. 3e); in the HPAs, the cover was 20.3%, 1.9%, 0%, 40.1%, 21.7% and 16%, and the contribution was 45.8%, 0.7%, 0%, 44.8%, 6.1% and 2.7%; in the NPAs, the cover was 6.9%, 1.3%, 0%, 45.7%, 30.7% and 15.5%, and the contribution was 26.4%, 3.8%, 0%, 56.5%, 12.7% and 0.6%. The difference in substrate contribution to *RI* across the three areas was statistically significant ($R = 0.26$, $P = 0.03$). The results suggested that the greater cover of rubble with low rugosity could partly explain the lower habitat complexity in the NTAs, compared with other two regions under less protection.

The contribution of coral to habitat rugosity

A total of 113 coral colonies from 28 species and 18 genera were measured. The *RI* of coral colonies

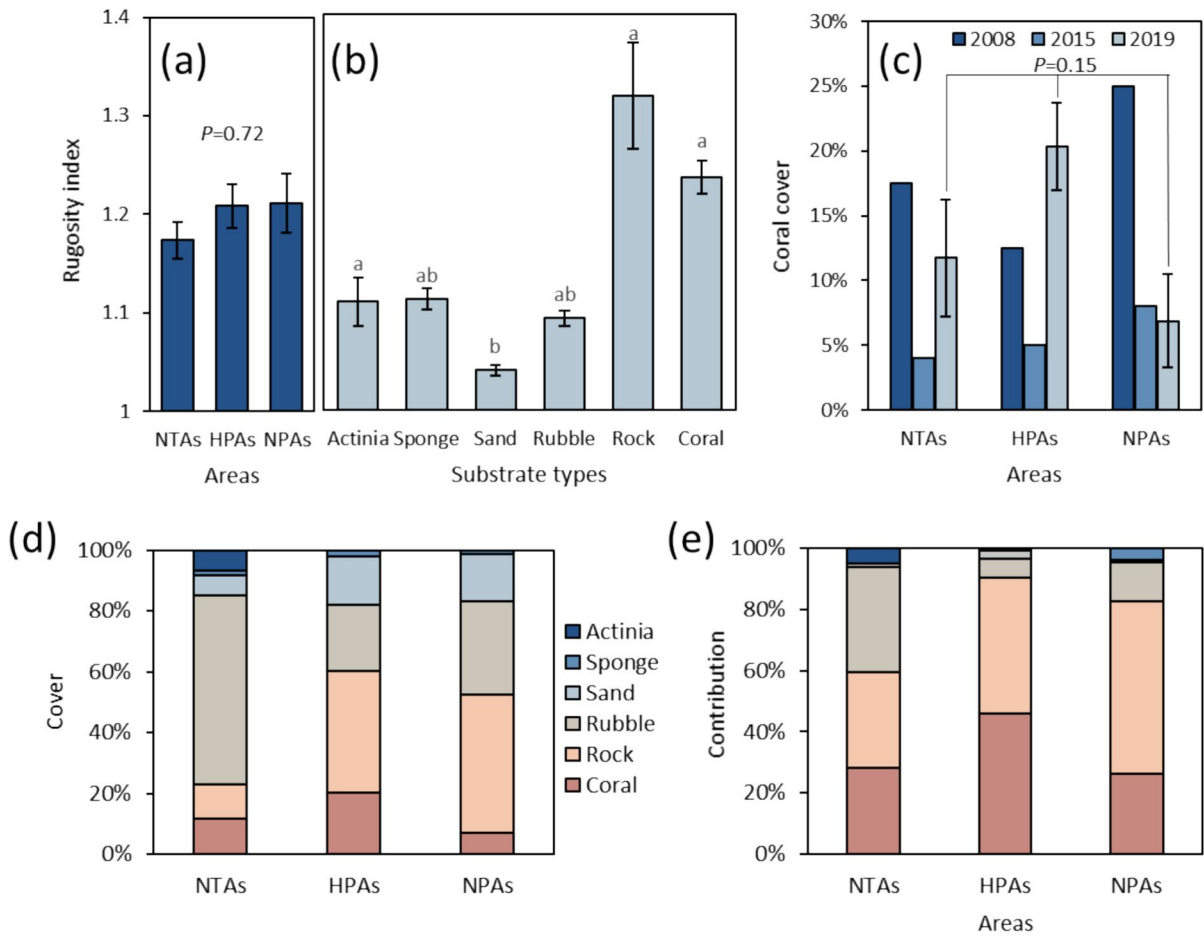


Fig. 3 Rugosity index of reef habitat in the three areas (a) including no-take areas (NTAs), habitat protection areas (HPAs) and no-protection areas (NPAs), as well as in six substrates (b). Changes in coral cover (c) from 2008 to 2019

across the three areas. Data for 2008 and 2015 are cited from Yu et al. (2019). Percentage cover (d) of six substrates and their contribution to rugosity (e) in the three areas. Mean and standard error (SE) are shown

averaged 1.24 (±0.17), ranging from 1.1 (*Echinophyllia aspera*) to 1.7 (*Acropora pruinosa*) (Fig. 4). The RI varied among coral morphology (Kruskal–Wallis $\chi^2=20.041$, $df=4$, $P<0.001$). Arborescent *Acropora* had the highest RI (1.7), followed by massive corals (1.3~1.5; *Porites*, *Galaxea*, *Plesiastrea*, *Favia* and *Platygyra*), foliose corals (1.1~1.3; *Pavona*, *Echinopora* and *Turbinaria*), sub-massive corals (1.1~1.25; *Favia*, *Goniastrea*, *Goniopora*, *Favites*, *Acanthastrea*, *Platygyra*, *Leptastrea* and *Lobophyllia*) and encrusting corals (1.1~1.2; *Echinophyllia*, *Montipora* and *Hydnophora*). The results suggested that the individuals of arborescent *Acropora* played an important role in constructing the three-dimensional structure of reefs, while those of foliose, sub-massive and

encrusting corals provide limited structural complexity for reefs. However, considering their relative coverages, massive corals contributed the most (15.6%) to habitat rugosity, followed by sub-massive (9.5%), foliose (5.3%), encrusting (2.4%) and arborescent corals (0.8%) in the Weizhou Island reef as a whole.

The contributions of corals to habitat rugosity varied among the regions. In the NTAs, foliose corals (5% cover) and sub-massive corals (4% cover) as the dominant groups (Fig. 5a) contributed 12.8% and 7.2%, respectively (Fig. 5b). Specifically, the contribution of foliose *Pavona decussata* and sub-massive *Lobophyllia flabelliformis* was 11% and 6%, respectively, while other corals contributed less than 5%. In the HPAs, sub-massive and massive corals were

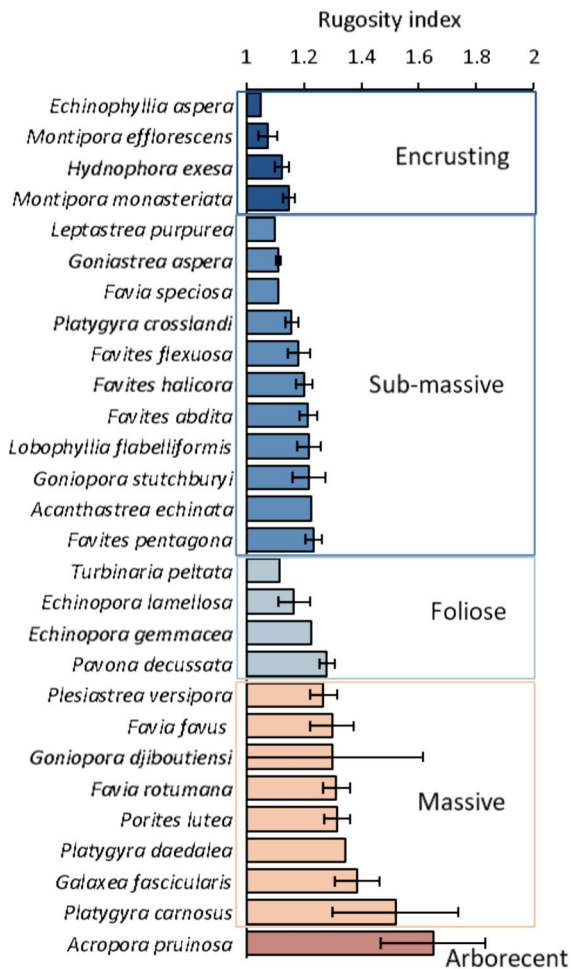


Fig. 4 Rugosity index of coral species in encrusting, sub-massive, foliose, massive and arborescent morphology. Mean and standard error (SE) are shown

the dominant species with covers of 11% and 6%, respectively, and contributed 21% and 18% to habitat rugosity. Massive *Porites lutea* had the greatest contribution (18.9%) to habitat rugosity, followed by sub-massive *Lobophyllia flabelliformis* and *Favites pentagona* (7%). In the NPAs, massive (3% cover) and sub-massive (2% cover) corals were the dominant groups, and contributed 19% and 4% to habitat rugosity, respectively, mainly through massive *Porites lutea* (8% contribution) and *Favia rotumana* (6% contribution). A few arborescent *Acropora* were found only on the reef slope of the HPAs, with covers ranging from 0.45% to 0.63%. Overall, in the coral community, the massive corals with relatively higher rugosity were primarily responsible for habitat

formation in the NPAs and HPAs. But the NTAs have to form the reef habitat, mainly depending on the foliose and sub-massive corals with relatively lower rugosity (massive vs foliose: $P=0.24$; massive vs sub-massive: $P=0.01$). This may also explain the lower structural complexity of the habitat in the NTAs compared with the other two regions.

Discussion

The MPAs, established since 2013, have achieved measurable benefits in restoring coral biomass in the Weizhou Island reef. Between 2015 and 2019, the living coral cover increased threefold in the NTAs, and fourfold in the HPAs. The coral cover in the NTAs was 1.7 times higher than that in the NPAs. A previous study revealed a significant recovery of coral larvae in the Weizhou Island from 2015 to 2018 ($F_{1,10}=6.05$, $P=0.03$), with coral recruitment increased by 3.4 times from 0.76 to 2.56 ind/m² (Yu, 2022). However, the values of *RI* averaged 1.2, and the *RI* was relatively lower in the NTAs (1.17) compared to the NPAs (1.20). A review summarized other studies on habitat rugosity at 150 stations around the world from 1972 to 2010 and showed that the values of the rugosity index averaged 1.46, ranging from 1.06 to 3.62 (Graham & Nash, 2013). Recent studies from 2007 to 2019 reported the rugosity index of habitats using multiple methods (Table 3). Except for reefs in Oahu having comparable values of *RI* (1.22) to the Weizhou Island reef, the other six locations revealed relatively higher values of *RI* (1.5~2.0) than that in the Weizhou Island reef. Especially, extremely high *RI* values (3.9~4.6) were observed in Danajon Bank reef in the Philippines. Since the establishment of MPAs in the Weizhou Island, the structural complexity of the habitat has remained a low level compared to other reefs around the world.

It is generally believed that coral cover is positively correlated with habitat complexity (Komyakova et al., 2013), because corals are the main builders of the three-dimensional structure of reefs (Perry & Alvarez-Filip, 2019). A high coral cover (20%) is expected to support a complex reef structure in the Indo-Pacific reef region (Graham & Nash, 2013), as seen in Danajon Bank reef, where an 80% coral cover yields a high value of *RI* (4.6) (Bayley et al., 2019a). However, in this study, there was no significant correlation

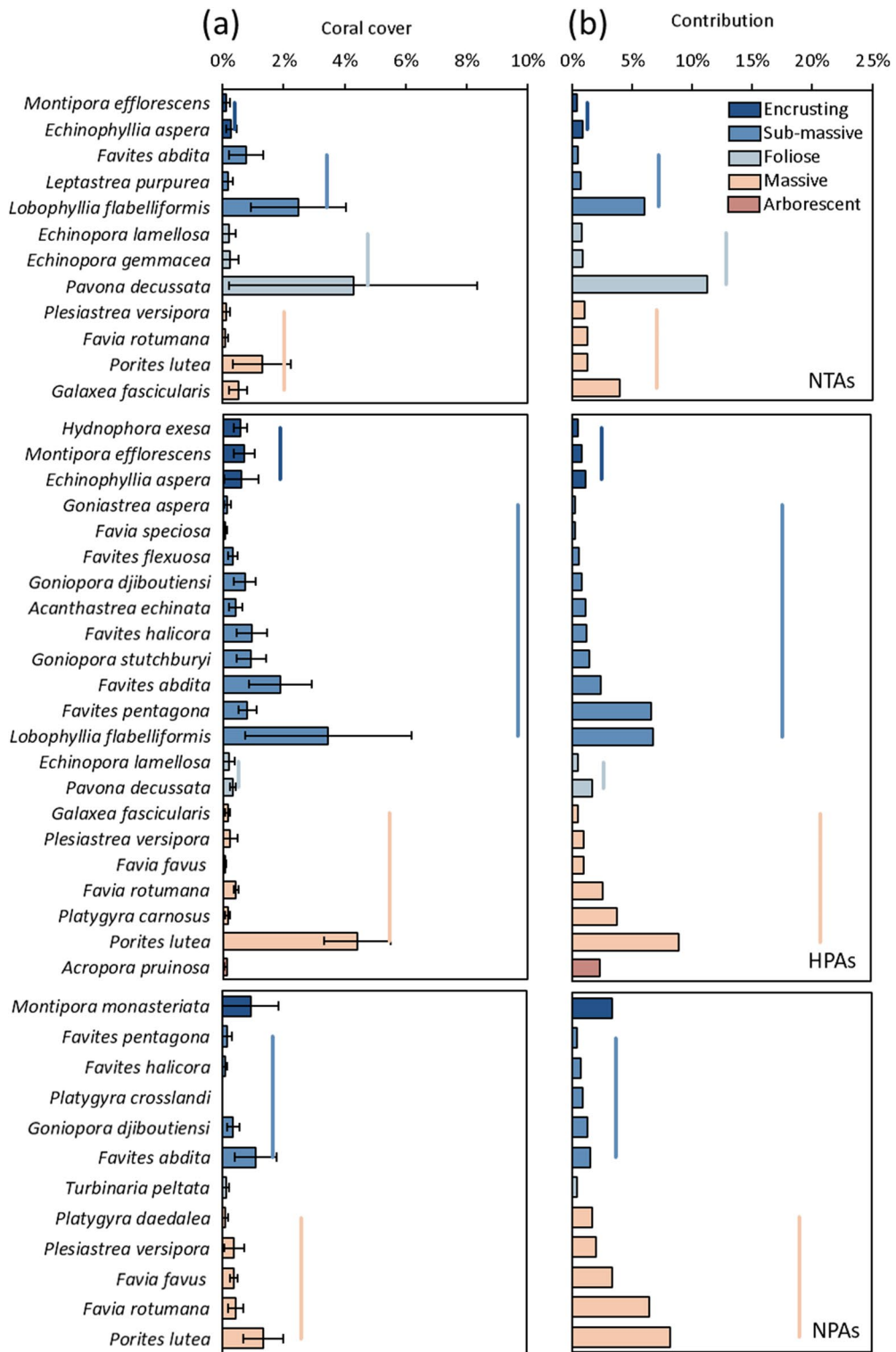


Fig. 5 Coral cover (a) of coral species in encrusting, sub-massive, foliose, massive and arborescent morphology, and their contribution to rugosity (b) across the three areas. Mean and

standard error (SE) are shown. The line represents the sum of values for each coral morphology

Table 3 Summary of coral reef rugosity from the literature

Location	Method	Rugosity	Coral cover	Time	Reference
Archipelago Los Roques, Caribbean	3D model created by digital images	1.7*	30%	2019	(Duvall et al., 2019)
Danajon Bank reef, Philippines	3D model created by digital images	3.9* 4.6* 1.9*	67% 80% 34%	2016	(Bayley et al., 2019a)
Myeik Archipelago, Myanmar	3D model created by digital images	1.65*	49%	2016	(Martina et al., 2019)
Ticao Island, Philippines	Point intercept contour line	1.5	No data	2013	(Yanovski et al., 2017)
Lizard Island, Great Barrier Reef	Contour distance estimated with wheels	1.5~2.0	No data	2017	(Richardson et al., 2017)
French Frigate Shoals, Hawaii	3D model created by digital images	1.52*	12.69%	2012	(Burns et al., 2015)
Lagoon of Lizard Island, Great Barrier Reef	Chain method	1.67	26.95%	2007	(Komyakova et al., 2013)
Cozumel Island	Chain method	1.49	16%	2008	(Alvarez-Filip et al., 2011b)
Oahu	Chain method	1.22	14.6%	2007	(Howard et al., 2009)
Weizhou Island, South China Sea	Chain method	1.20	14.82%	2019	This study

*Data have been transferred from 3D rugosity to 2D rugosity based on empirical formula (Bayley et al., 2019b): Rugosity (2D) = 0.606 × Rugosity (3D) + 0.465

between coral cover and habitat complexity (Fig. 2c). Moreover, the reef slope has a coral cover (18.53%) higher than the reef flat (11.12%), but both areas have a similar *RI* (1.20). The result is consistent with a previous study showing that the recovery of coral cover seems effective under ecological protection, but it does not necessarily lead to an improvement in habitat complexity and quality (Alvarez-Filip et al., 2011a). This mismatch likely suggests that the temporal inconsistency in recovery should be considered between biomass and complexity within restoration efforts.

Habitats often take a prolonged period to restore from disturbances, which may explain the limited outputs in many MPAs. During the initial phase of MPAs establishment in this study (six years), an increasing trend in the coral cover and recruitment indicated a recovery of biomass. However, the structural complexity of the reefs remained at a relatively low level, and no significant differences were observed across the three areas. Similar results have also been reported in other MPAs worldwide. For instance, the values of rugosity were similar without significant differences between the NTAs and adjacent NPAs in the reefs of Fiji (Ford et al., 2018). In the 66 reserves and 89 NPAs in the Caribbean Sea, the decline rates of the reef complexity index were

similar (Alvarez-Filip et al., 2011c). Over a span of 31 years and 139 sites throughout the Caribbean reefs, the *RI* varied widely, ranging from 1.05 to 2.0 at sites with similar coral cover (10%), and even from 1.05 to 3.5 at 40% coral cover (Alvarez-Filip et al., 2011a). Although short-term differences between unprotected and protected reefs are modest, long-term effects could be significant on the protected reefs (Guabiroba et al., 2022; Mouillot et al., 2016; Selig & Bruno, 2010). In this study areas (six years protection), in addition to *RI* values, coral cover ($F_{2,5} = 2.822$, $P = 0.15$) and recruitment ($F_{2,10} = 0.661$, $P = 0.54$; Yu, 2022) also did not differ across the three regions, which implies that the less variability in the rugosity and biomass do not improve the overall ecosystem services. In prolonged restoration, human interventions like MPAs and artificial reefs could potentially contribute to acceleration of rugosity improvement, when growing corals enable the formation of reef framework. Increasing rugosity has a positive correlation with fish density and biomass (with a 1.8 kg/250 m² increase in biomass for every 1.0 unit increase in complexity), and can enhance the overall ecosystem services (Fisher, 2023; Fontoura et al., 2020; Hall et al., 2023). This emphasizes that long-term conservation and management are required to gradually restore the complex structure of coral

reefs. The less variability in the rugosity is likely because that the structural complexity is influenced by substrate or coral composition (which needs a long period to restore) rather than coral cover alone (Richardson et al., 2017).

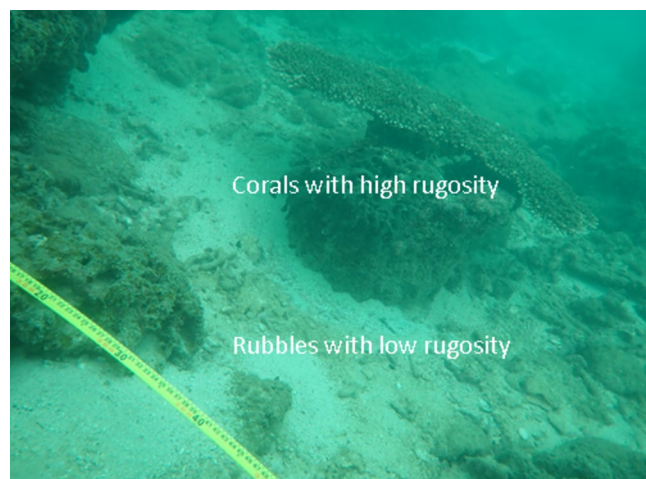
The structural complexity of reef habitat provided by the foundation substrate largely depends on the dominant taxa. In the NTAs, habitat complexity was the lowest, with rubbles as the primary substrate type (62% cover), accounting for 34.4% of habitat complexity; by contrast, the contributions of corals to the habitat complexity was only 28.3%. The skeletons of arborescent corals (e.g., *Acropora* spp.) may break down into rubbles after experiencing powerful disturbances (e.g., hurricanes), whereas massive coral skeletons typically erode in situ (Sheppard et al., 2002). These rubbles, without a three-dimensional structure, have relatively lower rugosity (1.09) compared to corals (1.24) (Fig. 6). The substrate mainly consists of rubbles rather than structurally complex corals, contributing little to the three-dimensional structure of the reef.

Arborescent corals generally have high structural complexity and provide a more efficient spatial structure than sub-massive corals (Gonzalez-Barrios & Alvarez-Filip, 2018). Indeed, as showed in Fig. 4, the *RI* of arborescent *Acropora* was the highest (1.7), higher than that of massive corals (1.3~1.5), as well as foliose, sub-massive and encrusting corals (<1.3). However, they only have a low contribution to habitat complexity in this study due to their small coverage. In the coral protected area of the Philippines, habitat complexity of the reef enhanced with an increase

in the cover of arborescent *Acropora* (Richardson et al., 2017). By contrast, massive and sub-massive corals with low topographical relief dominated the coral community in this study region, contributing to 20% of habitat complexity, while arborescent corals accounted for only 2.3% of the contribution to habitat complexity. Only a few arborescent *Acropora* were found on the reef slope of the HPAs, with a cover ranging from 0.45% to 0.63%. Arborescent corals were the dominant species in the coral community in the western part of Weizhou Island (with cover ranging from 50 to 80%) in the 1980s (Zou et al., 1988). Field surveys in 2005 and 2015 found a large amount of broken arborescent corals, with a cover of dead *Acropora* ranging from 25.39% to 31.4%, but the previously dominant arborescent *Acropora* species has been replaced by massive and sub-massive corals in the coral community (Yu et al., 2019). The loss of arborescent *Acropora* was a key factor in the loss of habitat complexity (Bellwood et al., 2004; Hughes et al., 2017).

The lack of fast-growing corals hinders the development of reef structure. Arborescent *Acropora* have an annual extension rate (90 mm year^{-1}) greater than massive *Porites* and foliose *Pavona* (10 mm year^{-1}) (Pratchett et al., 2015), thus providing complex frameworks more rapidly for reef-habitat organisms (Howard et al., 2009; Hughes et al., 2017). Without the fast-growing arborescent corals, the reconstruction of complex habitat structure may not grow quickly (Bozec et al., 2015). Therefore, it is not surprising that unrestored habitat was observed in this study after a 6-year period of protection by MPAs.

Fig. 6 A photo showing the difference between substrates with high rugosity and low rugosity



The restoration of habitat complexity may become a problem for many degraded reefs, where significant reductions in arborescent corals have been observed, e.g., in Daya Bay, Luhuitou of China (Yu, 2012). Although arborescent *Acropora*, owing to their rapid growth, once dominated Indo-Pacific reefs (Hughes et al., 2018) and the Caribbean Sea (Alvarez-Filip et al., 2009), reefs have continuously degraded over the past 40 years due to the loss of arborescent *Acropora*, resulting in a decrease in the *RI* from 2.5 to 1.2 (Alvarez-Filip et al., 2009). With the reduction of structurally complex and fast-growing corals, vertical reef growth and net carbonate production would be inhibited (Perry & Alvarez-Filip, 2019; Perry et al., 2018).

The contribution of corals to habitat complexity was only 25% in the NTAs, where foliose corals dominated in the coral community, contributing to the greatest proportion of habitat complexity (12.8%). Generally, foliose corals have a greater growth rate and structural complexity compared to massive and sub-massive corals (Perry et al., 2018). However, in this study, the *RI* of foliose corals (<1.3) was lower than that of massive corals (1.3–1.5). Similarly, reefs dominated by massive corals have greater habitat complexity than reefs dominated by foliose corals in Caribbean reefs, despite similar living coral covers in these reefs (Alvarez-Filip et al., 2011b).

Corals with phenotypic plasticity can exhibit specific morphology in specific conditions to improve their chances of survival (Veron, 2002). It could be speculated that foliose corals may decrease their structural complexity under specific environments, such as low light and strong currents. In this study region, due to the near-shore terrestrial inputs, the suspended matter in seawater increased to high levels, e.g., from 16.6 mg L⁻¹ in 2014 to 20.5 mg L⁻¹ in 2016 (Liang & Peng, 2018), with low visibility (3.5–10.2 m; Li et al., 2019). Moreover, this study region is situated at a relatively high latitude, receiving less solar radiation than tropical reefs. Foliose corals could spread horizontally to improve the utilization of light (Hoogenboom et al., 2008) and maximize their energy capture (Sommer et al., 2014). On the other hand, the high current speeds (35–60 cm s⁻¹) in the NTAs potentially affect coral morphology. In windward condition, waves and strong currents become the predominant influences on coral growth (Scoffin et al., 1992), and the structural complexity

of corals is 25% lower than in bays and lagoons with weak waves or currents (Todd, 2008). These findings suggest that foliose corals tend to alter their morphology to adapt to low light and strong currents, thereby decreasing their structural complexity.

MPAs may protect coral reefs from anthropogenic disturbances, but inevitable hurricanes still threaten reef ecosystems (Alvarez-Filip et al., 2011c). In the Caribbean Sea, habitat complexity decreased in 66 protected areas and 89 non-protected areas after hurricane events (Alvarez-Filip et al., 2011c). The reduction rate of structural complexity in hurricane-affected reefs was over five times higher than in unaffected areas. In the Weizhou Island from 2014 to 2018, the local reefs have experienced four typhoons and subsequently collapsed (Li et al., 2019). Hurricanes are also an important factor in reef collapse and habitat destruction (Alvarez-Filip et al., 2013). Furthermore, bioerosion potentially accelerates the destruction of the reef framework (Bruno et al., 2019). Internal bioerosion of coral skeletons has been observed in the Weizhou Island with an erosion intensity of 7.08% (Chen et al., 2013). Bioerosion could be promoted by nutrient enrichment. The concentration of dissolved inorganic nitrogen increased from 2.7 to 5.9 μmol L⁻¹ (1990–2015), and then increased by 1.3 times (2015–2016) (Liang & Peng, 2018). Additionally, MPAs with limited fishing pressure are considered beneficial for the recovery and resilience of coral populations, through the removal of spatial competitors (e.g., macroalgae) by grazing herbivorous fish (Mumby & Harborne, 2010). However, herbivory may also physically accelerate bioerosion on the reef structure (Hutchings, 1986; McClanahan, 1994). The increased bioerosion may explain the relatively low habitat complexity in the NTAs, where fishing activity has been completely prohibited, compared to the NPAs and HPAs. Thus, the reef structure weakened by bioerosion becomes vulnerable to waves, especially in near-shore seawater (Alvarez-Filip et al., 2013; Chen et al., 2013).

Conclusion

This study provided a quantitative method for analyzing the quality of reef habitat, by combining substrate composition and coral morphology with topographic relief. A case study of the coral reefs

of Weizhou Island showed that the MPAs enhance coral cover after six years of protection, the benefits of restoring the structural complexity of the reef habitat remained insignificant in the short term. The lower rugosity of the coral reefs with strict protection measures indicated less habitat complexity and quality, which may not be beneficial for harboring large quantities of marine organisms. This is likely because corals contribute a smaller portion to habitat complexity than other substrate types, e.g., rubble. Moreover, due to the lack of fast-growing, arborescent corals, the coral reef has to form its framework, mainly depending on slow-growing corals with lower rugosity, e.g., foliose and sub-massive corals. Restoration of the structural complexity of coral habitats relies on the morphology of the corals and the composition of corals of different morphotypes. This study thus suggests that quantifying habitat structural complexity, in addition to coral biomass, may better assess the protection performance on coral reefs. Coral species composition, especially fast-growing corals with high rugosity like *Acropora*, should be prioritized when reconstructing reef framework in prolonged restoration projects.

Author contribution Wang Y.Z. performed experiments and wrote the main manuscript text. Li Y.X. analyzed data and wrote the main manuscript text. Yu K.F. and Chen X.Y. reviewed the manuscript.

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Data availability Data are available on request from the authors.

Declarations

Ethics approval All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors and are aware that with minor exceptions, no changes can be made to authorship once the paper is submitted.

Consent to participate All authors have given consent to their contribution.

Competing interests The authors declare no competing interests.

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