



## Intergeneric and geomorphological variations in Symbiodiniaceae densities of reef-building corals in an isolated atoll, central South China Sea

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### ABSTRACT

The healthy status of corals in the isolated atolls of the central South China Sea (SCS) remains unclear. Symbiodiniaceae density (SD) can effectively reflect the thermal tolerance and health of hard corals. Here, the SDs of 238 samples from the Huangyan Atoll (HA) were analyzed. The results revealed significantly intergeneric and geomorphological differences in SD. Intergeneric variation may reflect that corals with high SD have stronger thermal tolerance. Geomorphic analysis showed that the SDs at the outer reef slope were higher than in the lagoon. Hydrodynamics and sea surface temperature were likely the main influencing factors. Most notably, corals in SCS HA had higher SDs than those at neighboring reefs, indicating that their thermal tolerance were strong, which may be related to HA's local upwelling. These results suggest that the HA has the potential to serve as a refuge for corals, but increasing human disturbance limit its function.

### 1. Introduction

Coral reef ecosystems possess extremely high biodiversity and economic value (Bellwood et al., 2004; Costanza et al., 2014; Anthony, 2016). In their ecosystem, reef-building corals mainly rely on their relationship with the symbiotic dinoflagellates (i.e., Symbiodiniaceae) that provide them with essential nutrients for growth, calcification, and reproduction (Li et al., 2008; Oliver and Palumbi, 2011). Nevertheless, the increasing frequency and severity of abnormal sea surface temperatures (SST) and other local stresses could disrupt this symbiotic relationship. These can cause the Symbiodiniaceae to be expelled (Hoegh-Guldberg, 1999; Ban et al., 2014), which can eventually lead to coral bleaching and even mortality (Baker et al., 2004; Hughes et al., 2017; Hughes et al., 2018). Generally, this process also affects the growth and reproduction of reef-building corals, increases their susceptibility to various diseases, posing a serious threat to reef survival (Douglas, 2003; Hoegh-Guldberg et al., 2007; Baker et al., 2008; McClanahan et al., 2014). Furthermore, coral susceptibility to thermal bleaching is related to Symbiodiniaceae density (SD), and the higher the SDs, the stronger the resistance to bleaching (Baker et al., 2008; Li et al., 2008; Xu et al.,

2017). Therefore, SD is considered to be a key indicator of corals' thermal tolerance and health (Jones, 1997; Wooldridge, 2014).

A growing number of studies highlight the influence of environmental factors on SD, including SST, salinity, solar radiation, nutrients, hydrodynamic regimes, and human activities (Smith et al., 2005; Wiedenmann et al., 2013; Ben-Zvi et al., 2019), leading to variations of SDs on interspecific, spatial and temporal scales (Xu et al., 2017; Qin et al., 2019a). In general, coral species that are more thermally tolerant or more adaptable exhibit higher SDs and are healthier (West and Salm, 2003; Berkelmans and van Oppen, 2006; Muir et al., 2015; Xu et al., 2017; Qin et al., 2019b). For example, in different species, SDs of branching *Acropora* species, which are the most vulnerable to bleaching, have been shown to be significantly lower than those of the massive corals (Marshall and Baird, 2000; Xu et al., 2017). Additionally, analyses of the SDs in different regions revealed that corals showed higher SDs in environments that could reduce the threat of thermal exposure (Qin et al., 2019a). Nevertheless, corals in shallower lagoons can also adapt to the fluctuating environmental conditions they endure on a daily basis and have become more resistant to bleaching stress, showing higher SDs (Grimsditch et al., 2010; Barshis et al., 2013). Variations in SDs

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therefore, reflect the corals' response to different environments (Woolridge, 2014; Xu et al., 2017; Qin et al., 2019a, 2019b). Under the threat of global warming, it is necessary to identify more representative reefs worldwide by SD and, for each reef, describe the traits of present species, and the variation in local SST and current environmental conditions (Logan et al., 2014).

The South China Sea (SCS) with the highest coral diversity, borders the Coral Triangle, is an important part of the world's coral reefs (McManus et al., 2010; Yu, 2012). However, corals throughout the SCS have experienced several abnormal temperature events, leading to extensive coral bleaching and significant mortality, and its reefs are rapidly degrading (Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Zhao et al., 2012). Additionally, the El Niño events during 2015–2016, which was one of the most severe episodes since 1998, combined with the risks of overfishing, sedimentation, and marine-based pollution, seriously threatening the health of coral reefs in this area (Burke et al., 2011; Zhao et al., 2016; Tkachenko and Soong, 2017). Therefore, recent studies have focused on determining the SD in corals of nearly all of the coral reefs in the SCS, as these reflect, to some extent, the health status of coral reefs in the SCS (Li et al., 2008; Xu et al., 2017; Qin et al., 2019a). However, little attention has been paid to the coral reefs in the Huangyan Atoll (i.e., Scarborough Shoal), especially their Symbiodiniaceae of corals (Zhao et al., 2013, 2016; Ke et al., 2016; Li et al., 2018). This serious knowledge gap is detrimental to the evaluation and protection of the entire coral reef ecosystems of the SCS (Hariithsa et al., 2005; Berkelmans and van Oppen, 2006). Furthermore, studies have also found that despite the high susceptibility of reefs on remote atolls in the SCS to extensive bleaching and mortality due to various stressors, the potential for recovery of these isolated reefs is remarkable (Mora et al., 2016; Safaie et al., 2018; Chen et al., 2019b; Tkachenko et al., 2020). In short, the lack of research limits our ability to understand the ecological status of these reefs and predict their fate in a future subjected to increased warming and otherwise aspects of a changing climate. It may also overlook some reefs with potential functions.

The objective of this study is thus to analyze the SDs of corals collected in the Huangyan Atoll in May 2015, and to explore the effects of abnormally high temperatures on the coral reefs in this region,

thereby, assessing the current ecological status and developmental trend of reef-building corals in the Huangyan Atoll under the climate change scenario.

## 2. Material and methods

### 2.1. Study sites

The Huangyan Atoll (HA; 117°40'–117°52'E, 15°05'–15°13'N), also named Scarborough Shoal or Democracy Reef, is located in the central SCS (Fig. 1). Its coral reef is roughly triangular, partially encircles a lagoon, and comprises an area of approximately 133 km<sup>2</sup> with depths of 10–20 m. In the southeast, there is a passage (approximately 370 m wide and 3–11 m deep) connecting the lagoon and the open sea. Due to the micro-tidal regime (approximately 1.2 m), many coral reefs are submerged at high tide (Li et al., 2018). In addition, extensive patches of healthy corals are scattered throughout the reef flats and are most abundant on the outer reef slope. Here, the corals are exposed to well-flushed and highly turbulent waters and are relatively undisturbed by local conditions. In contrast, the lagoon environment is generally quiet and shallow (mostly 9–11 m, with a maximum depth of 19.5 m). In this area, most of the substrate is sand, mud and reef, and water exchange with the open sea occurs only through the passage in the southeast or during high or low tides (Lowe and Falter, 2015). Thus, the lagoon's hydrodynamic regime is relatively weak, and a particular local environment is established within it. Nonetheless, it is important to note that these corals are still in relatively good health (Ke et al., 2016, 2018; Li et al., 2018).

The circulation of the HA is mostly driven by the southwest monsoon in Summer, which pushes the water northward (Hu et al., 2000). Furthermore, there exists an unstable eddy in the north of the SCS, which may also reach the HA in Summer (Fig. S1 in the supporting information) (Fang et al., 1998; Hu et al., 2000). Moreover, according to the NOAA database (<https://coralreefwatch.noaa.gov/satellite/composites/index.php>), the average annual SST during 2005–2015 was 28.6 °C, and showed an overall upward trend. In particular, relatively high SST appeared in the summers of 2010, 2013, 2014, and 2015

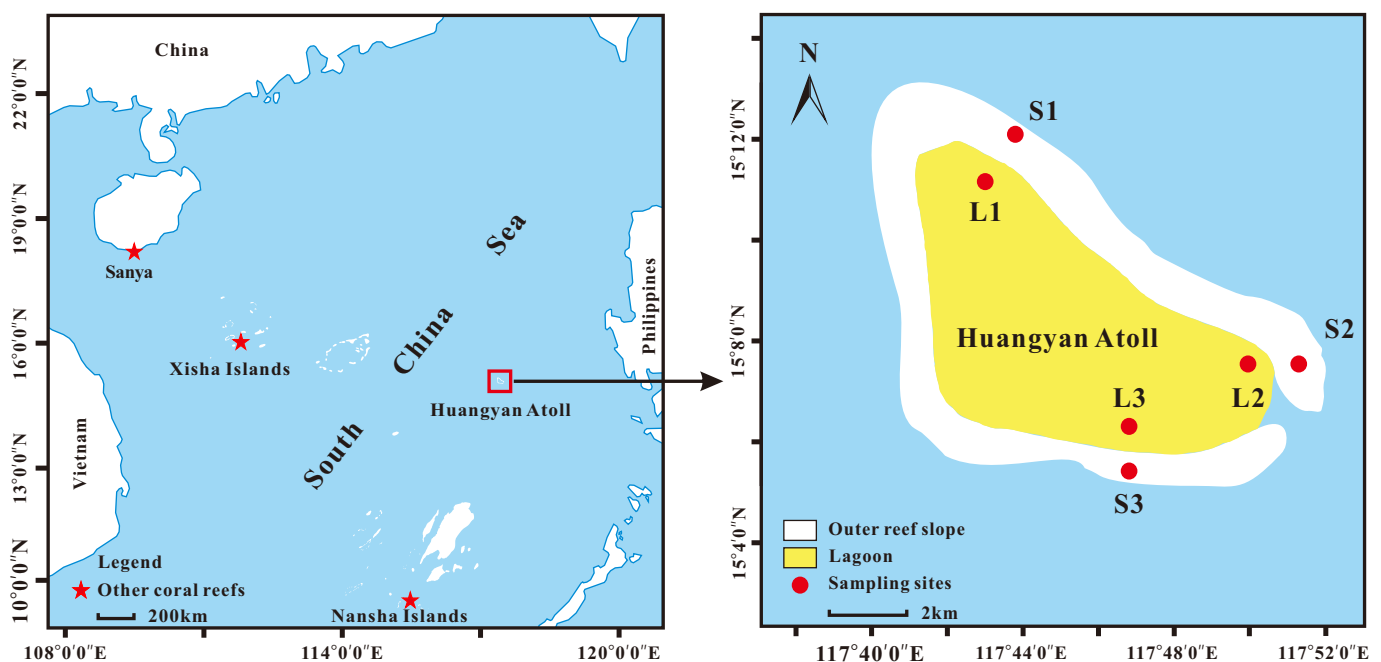


Fig. 1. Map of the study sites (right) and location of the Huangyan Atoll (HA) and several coral reefs in the South China Sea (left). Several coral reefs in the South China Sea include the Nansha Islands, the Xisha Islands and Sanya in Hainan Island. A total of five sites were sampled within the HA, two of which were located in the lagoon (L2, L3), whereas the remaining three were located on the outer reef slope (S1–S3).

(Fig. S2). The average monthly SST in 2015 varied from 26.8 °C to 30.1 °C, and the SST reached a maximum of 30.7 °C in June (Fig. S2). In addition, the hotspot map (Fig. S3) shows that the HA began to have high SST anomalies in the range of 0.5–0.75 °C since May 7, 2015. The warmest month throughout 2015 for the HA was June, when the anomaly ranged from 1.5–1.75 °C. During our investigation (May 19 to 24), this region was in the middle stage of an extremely high SST event (Goreau et al., 2010), and an on-the-spot measurement recorded SST >

31 °C (the SST of the outer reef slope and the lagoon were 31.2 °C and 31.5 °C, respectively), which is close to the highest SST period in 2015.

## 2.2. Coral sampling

In the HA, sampling was conducted across the northeastern, southeastern, and southern regions of the outer reef slope and lagoon (Fig. 1). Three different depths (2 m, 10 m and 15 m) were set at each station in

**Table 1**  
Symbiodiniaceae densities in the corals collected from the different geomorphology of the Huangyan Atoll.

Family	Genus	Species	Symbiodiniaceae density ( $\times 10^6$ cells.cm <sup>-2</sup> )	Number of samples	Geomorphological sites	Morphology	
Poritidae	Porites	<i>P. lutea</i>	4.74 ± 0.32	19	Outer reef slope	Massive	
			3.35 <sup>a</sup>	1	Lagoon	Massive	
		<i>P. lobata</i>	5.84 ± 0.42	19	Outer reef slope	Massive	
Faviidae	Favia	<i>F. speciosa</i>	4.32 ± 0.42	3	Lagoon	Massive	
		<i>F. palauensis</i>	4.64 ± 0.51	2	Outer reef slope	Massive	
		<i>F. stelligera</i>	1.68 ± 0.05	2	Outer reef slope	Massive	
		<i>F. matthaii</i>	6.35 ± 1.05	2	Outer reef slope	Massive	
			3.58 ± 0.18	2	Outer reef slope	Massive	
	Favites	<i>F. halicora</i>		3.06 ± 0.16	3	Lagoon	Massive
			<i>F. pentagona</i>	5.11 ± 0.31	5	Outer reef slope	Massive
			<i>F. flexuosa</i>	3.1 <sup>a</sup>	1	Outer reef slope	Massive
			<i>F. abdita</i>	3.7 <sup>a</sup>	1	Outer reef slope	Massive
				4.66 ± 0.72	4	Outer reef slope	Massive
				2.77 ± 0.06	2	Outer reef slope	Massive
	Goniastrea	<i>G. aspera</i>		2.96 ± 0.26	5	Outer reef slope	Massive
			<i>G. yamanarii</i>	3.35 ± 0.16	7	Outer reef slope	Massive
			<i>G. pectinata</i>	3.34 ± 0.93	3	Outer reef slope	Massive
			<i>G. retiformis</i>	3.78 ± 0.46	2	Outer reef slope	Massive
	Leptoria	<i>L. phrygia</i>		3.77 ± 0.76	3	Outer reef slope	Massive
	Platygyra	<i>P. crosslandi</i>		3.41 ± 0.38	6	Outer reef slope	Massive
			<i>P. sinensis</i>	4.29 ± 0.41	4	Outer reef slope	Massive
	Plesiastrea	<i>P. curta</i>		3.73 ± 0.58	4	Outer reef slope	Massive
<i>P. versipora</i>			3.18 ± 0.47	3	Lagoon	Encrusting	
Cyphastrea	<i>C. serailia</i>		1.6 ± 0.1	2	Outer reef slope	Encrusting	
		<i>M. turgescens</i>	1.5 ± 0.31	2	Outer reef slope	Encrusting	
Acroporidae	Montipora	<i>M. efflorescens</i>	3.86 ± 0.32	2	Outer reef slope	Encrusting	
		<i>M. turgescens</i>	2.77 <sup>a</sup>	1	Outer reef slope	Encrusting	
		<i>M. foveolata</i>	1.21 <sup>a</sup>	1	Outer reef slope	Encrusting	
		<i>M. grisea</i>	3.84 ± 0.33	3	Outer reef slope	Encrusting	
		<i>M. danae</i>	2.41 <sup>a</sup>	1	Outer reef slope	Encrusting	
		<i>M. digitata</i>	2.8 ± 0.11	5	Outer reef slope	Branching	
		Acropora	<i>A. nasuta</i>	3.09 ± 0.23	3	Outer reef slope	Branching
			<i>A. humilis</i>	2.36 <sup>a</sup>	1	Outer reef slope	Branching
			<i>A. echinata</i>	1.37 <sup>a</sup>	1	Lagoon	Branching
			<i>A. florida</i>	2.55 <sup>a</sup>	1	Outer reef slope	Branching
	<i>A. aculeus</i>		2.52 <sup>a</sup>	1	Outer reef slope	Branching	
	<i>A. cytherea</i>		1.61 ± 0.3	2	Outer reef slope	Branching	
			1.29 <sup>a</sup>	1	Lagoon	Branching	
	<i>A. rosaria</i>		2.35 ± 0.32	2	Outer reef slope	Branching	
	<i>A. selago</i>		1.58 ± 0.26	6	Outer reef slope	Branching	
			1.58 ± 0.09	2	Lagoon	Branching	
	<i>A. brueggemanni</i>		1.77 ± 0.53	2	Outer reef slope	Branching	
			0.52 ± 0.11	3	Lagoon	Branching	
	<i>A. azurea</i>		2.02 ± 0.25	3	Outer reef slope	Branching	
	<i>A. cerealis</i>		2.39 <sup>a</sup>	1	Outer reef slope	Branching	
	<i>A. abrotanoides</i>		4.18 <sup>a</sup>	1	Outer reef slope	Branching	
	<i>A. verweyi</i>		3.3 ± 1.69	2	Outer reef slope	Branching	
	<i>A. gemmifera</i>		2.54 ± 0.12	10	Outer reef slope	Branching	
	<i>A. palifera</i>	1.74 ± 0.51	2	Outer reef slope	Branching		
	<i>A. digitifera</i>	2.84 ± 0.54	3	Outer reef slope	Branching		
	<i>A. robusta</i>	2.57 <sup>a</sup>	1	Outer reef slope	Branching		
	<i>A. hyacinthus</i>	2.78 ± 0.39	6	Outer reef slope	Branching		
<i>A. pulchra</i>	0.76 ± 0.14	2	Lagoon	Branching			
<i>A. muricata</i>	1.21 ± 0.03	2	Lagoon	Branching			
Pocilloporidae	Pocillopora	<i>P. verrucosa</i>	1.98 ± 0.16	18	Outer reef slope	Branching	
		<i>P. meandrina</i>	2.14 ± 0.17	16	Outer reef slope	Branching	
		<i>P. woodjonesi</i>	2.06 ± 0.17	17	Outer reef slope	Branching	
		<i>P. eydouxi</i>	1.52 ± 0.16	6	Outer reef slope	Branching	
Total			3.21 ± 0.11	217	Outer reef slope		
			2.19 ± 0.30	21	Lagoon		
			3.12 ± 0.11	238			

Note.

<sup>a</sup> Indicates that there is only one sample, and the variance cannot be calculated.

the outer reef slope (S1, S2, S3), whereas two depths (2 m, 4 m) were set at each station in the lagoon (L2, L3). During 19 to 24 May 2015, coral samples with a surface area of approximately 50 cm<sup>2</sup> were collected from each depth at each sample site by diving. These samples were immediately placed in a sealed container at a temperature below 0 °C.

### 2.3. Determination of Symbiodiniaceae densities

We followed the standard procedure for determining coral SDs (Li et al., 2008; Xu et al., 2017; Qin et al., 2019a). The samples with a surface area of about 50 cm<sup>2</sup> were sealed into a container and Symbiodiniaceae were separated from coral skeletons using a high-pressure water jet (WaterPik irrigator) powered by on 0.45 μm filtered seawater (Fitt et al., 2000; Zhang et al., 2006). To achieve thorough homogenization, we vigorously shook the rinsing liquid containing Symbiodiniaceae and placed it into a measuring barrel. The slurry was then homogenized and subsampled into four 3-ml aliquots, then centrifuged at 4000 rpm for 3 min. SDs were calculated using replicate hemocytometer counting (n = 8) under a microscope. The surface areas of the coral skeletons were determined based on the relationship between the aluminum foil weight and the surface area. Moreover, for further analysis and comparison, we collected data from previous studies regarding the SDs of other coral reefs in the SCS, including the Nansha Islands (i.e., Spratly Islands, 9–11°N, SST: ~23 °C), Xisha Islands (i.e., Paracel Islands, 15–17°N, SST: ~24.6 °C), and Sanya in Hainan Island (18–20°N, SST: ~25 °C; Fig. 1) (Qin et al., 2019a).

### 2.4. Data analyses

All data were statistically analyzed using SPSS version 22. A two-way factorial analysis of variance (ANOVA) was used to test the effect of geomorphological differences on the response variables. Levene's, Durbin-Watson's, and Shapiro-Wilk's tests were used to assess whether the data met the assumptions of homogeneity, normality, and independence, respectively. Subsequently, the intergeneric, geomorphological and spatial diversities of SDs were investigated by one-way ANOVA tests, and the Student-Newman-Keuls post-hoc test was used to examine significant differences between the data. All data were presented as mean ± standard error (SE), and the statistical significance level was set at p < 0.05 for all analyses.

## 3. Results

A total of 238 coral samples comprising 51 species of 11 genera within four families collected from the HA were analyzed in the present study (Tables 1 and S1). The SDs obtained for all species and geomorphologies ranged from  $0.76 \times 10^6$  to  $6.35 \times 10^6$  cells.cm<sup>-2</sup>, with an average of  $3.12 \pm 0.11 \times 10^6$  cells.cm<sup>-2</sup> (n = 238), among which the *Favia matthaii* exhibited the highest average SDs while *Acropora pulchra* displayed the lowest. Overall, SDs varied greatly between corals in different genera and within each geomorphology, but an interaction effect was not observed between coral SDs of the same genera in different geomorphologies (Table 2, two-way ANOVA, geomorphology: F = 11.01, p < 0.001; genera: F = 24.96, p = 0.001; interaction: F = 0.27, p > 0.05).

**Table 2**

Two-way ANOVA results on the effects of geomorphology and coral genera on Symbiodiniaceae densities.

Symbiodiniaceae densities ( $\times 10^6$ cells.cm <sup>-2</sup> )			
	df	F	P
Geomorphology (G1)	(1,124)	11.01	<0.001
Genera (G2)	(3,124)	24.96	=0.001
G1 × G2	(3,124)	0.27	>0.05

Abbreviations: ANOVA, analysis of variance; df, degrees of freedom.

For corals of different genera and morphology, their SDs were markedly different (Table 1; Fig. 2, ANOVA, p < 0.001). Clearly, the SDs were significantly higher in *Porites* than in *Cyphastrea*, *Montipora*, *Acropora*, and *Pocillopora*. Furthermore, the SDs in *Cyphastrea* and *Pocillopora* significantly differed (Fig. 2). In general, SDs also significantly differed between corals of different morphologies (Fig. 2, ANOVA, p < 0.001). The SDs in massive corals (such as *Porites* and *Favia*) were the highest ( $4.37 \pm 0.16 \times 10^6$  cells.cm<sup>-2</sup>, n = 99), followed by those in encrusting corals ( $2.96 \pm 0.27 \times 10^6$  cells.cm<sup>-2</sup>, n = 19) and branching corals ( $2.11 \pm 0.08 \times 10^6$  cells.cm<sup>-2</sup>, n = 120). Specifically, SDs in massive corals were more than twice those of branching corals. Altogether, these results suggest that there are significant differences in SDs between different coral species.

With regard to different geomorphologies, the average SDs of corals were higher on the outer reef slope ( $3.21 \pm 0.11 \times 10^6$  cells.cm<sup>-2</sup>, n = 217) than in the lagoon ( $2.19 \pm 0.30 \times 10^6$  cells.cm<sup>-2</sup>, n = 21), showing considerable variation (Fig. 3, ANOVA, p = 0.001). In detail, any genera in the outer reef slope, such as *Porites*, *Acropora*, *Cyphastrea*, and *Favites*, consistently showed higher SDs than the same genera within the lagoon (Table 1, Fig. 3).

Compared with the data from the other reefs in the SCS (Fig. 1), such as the Nansha Islands, at lower latitude, and the Xisha Islands and Sanya at higher latitudes (Qin et al., 2019b), we found the SDs of corals in the HA were at a relatively high levels, showing significant spatial variation (Fig. 4, ANOVA, p < 0.001). Specifically, the SDs of corals in the HA were significantly higher than those in the Nansha or Xisha Islands. Although their SDs were lower than those of Sanya, there was no significant difference (Fig. 4). In short, the SD varies according to coral species, geomorphological environment and location.

## 4. Discussion

### 4.1. Intergeneric variation of SDs and their relationships with coral tolerance to thermal stress

The results of the present study reveal that SDs vary greatly between coral genera in the HA, which is consistent with previous findings in the SCS (Li et al., 2008, 2011; Xu et al., 2017). In general, the SD among coral genera is often linked to their thermal tolerance. Corals with strong tolerance to thermal stress tend to have high levels of SDs (Wooldridge, 2014; Xu et al., 2017). Therefore, we suggest that the SD variations in HA can also reflect the thermal tolerance of corals.

This relationship can be explained using previous empirical evidence (Loya et al., 2001; McClanahan, 2004; Wooldridge, 2014). On the one hand, corals species with high SDs are more resistant to thermal stress (Marshall and Baird, 2000; Xu et al., 2017). For example, the thermal tolerance of massive corals is greater than that of branching species, showing higher SDs. Surviving branching corals have relatively high SDs in comparison with branching species during bleaching events (Glynn, 1993; Stimson et al., 2002). On the other hand, the corals with higher SDs also have substances (Salih et al., 2000; Lesser, 2006; Baird et al., 2008; Wang, 2012; Rosic et al., 2015) or structures (Liang et al., 2017; Qin et al., 2020) that enhance the tolerance of corals to thermal stress, such as thicker tissue (Qin et al., 2020) and more abundant bacterial diversity (Liang et al., 2017; Chen et al., 2019a). In our study, SDs were significantly higher in massive species (e.g., *Porites lutea*, *Porites lobate*, and *Pavona varians*) than in encrusting species (e.g., *Montipora* and *Cyphastrea*) or branching species (e.g., *Acropora selago* and *Acropora pulchra*). As such, these findings from present and previous studies illustrate that the thermal tolerance of corals is positively correlated with their SDs. Hence, the thermal tolerances of corals in the HA can be assessed using their SDs.

### 4.2. Geomorphological differences between SDs and their drivers

Our analysis demonstrates the SDs of corals are higher in the outer

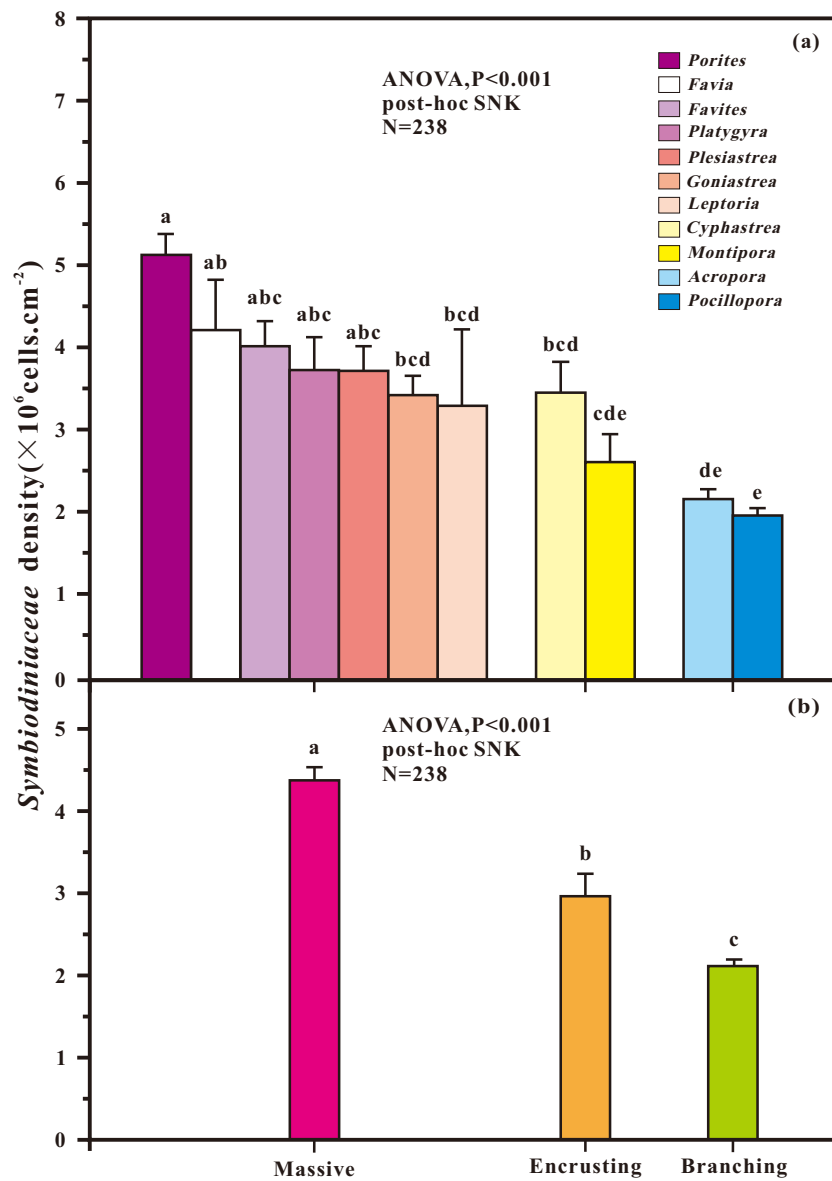


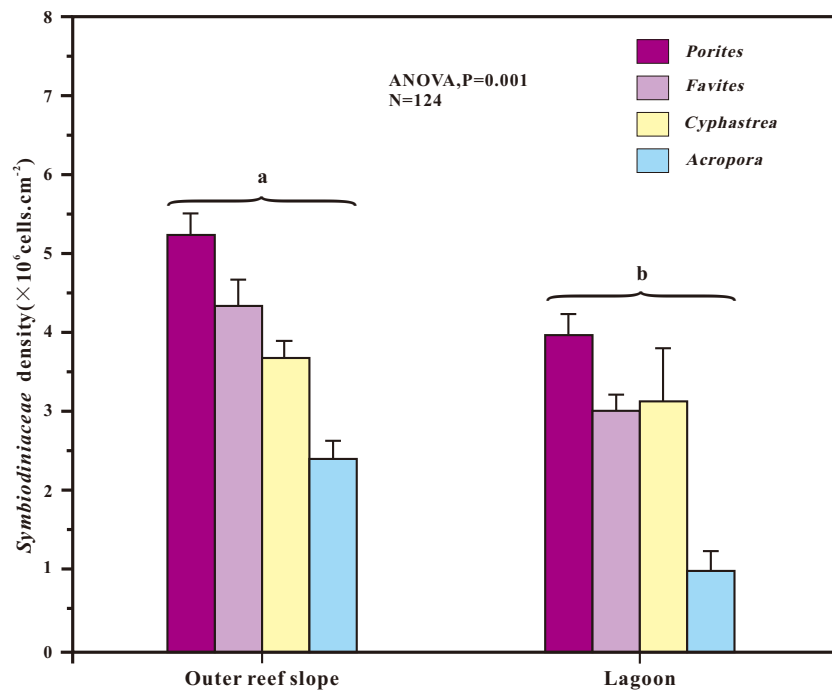
Fig. 2. Intergeneric variation in Symbiodiniaceae densities (SDs) of corals in the Huangyan Atoll. The SDs significantly differed among coral genera (a) and morphology (b). All error bars are standard errors, and letters above bars (e.g., a, b, and c) denote statistical differences among coral genera and morphologies in regards to SDs (Student–Newman–Keuls test, P < 0.05).

reef slope than in the lagoon (e.g., *Porites*, *Acropora*, *Cyphastrea* and *Favites* had the higher SDs in the outer reef slope, respectively), appears highly variable between geomorphological regions. This implies that the SDs of corals vary in their responses to the geomorphic environment. The geomorphological differences of SDs in the HA may be related to characteristics of the local environment, such as the hydrodynamic condition, SST and solar radiation (Finelli et al., 2006; Schmidt et al., 2016; Rogers et al., 2017).

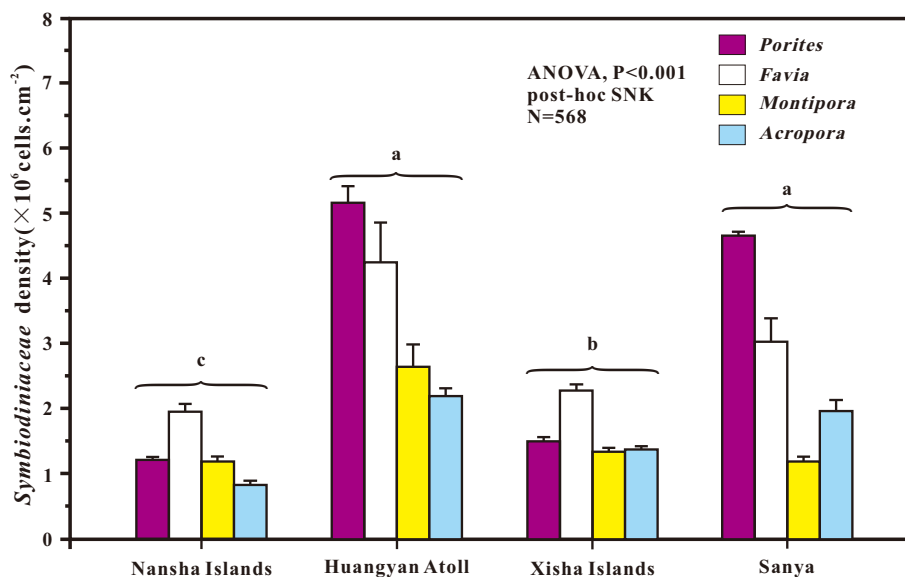
With regard to hydrodynamics, in the lagoon, the hydrodynamic conditions of this shallow and closed local environment are relatively weak, which could easily amplify damage to the photosynthetic system of the Symbiodiniaceae from solar radiation (Nakamura et al., 2005), resulting in the reduction of the passive diffusion of heat from the coral surface, and finally exacerbating the expulsion of Symbiodiniaceae (Nakamura and van Woesik, 2001; Suzuki et al., 2008; Sawall et al., 2014). By contrast, the outer reef slope, with its well-flushed and highly turbulent waters, could reduce the effects of light inhibition and thermal stress on Symbiodiniaceae (Finelli et al., 2006; Suzuki et al., 2008;

Schmidt et al., 2016; Rogers et al., 2017), which in turn exhibiting higher SDs in the outer reef slope than in the lagoon.

In addition to hydrodynamics, the differences in SST and solar radiation between the outer reef slope and the lagoon may also affect the SD (Fitt et al., 2000). During our investigation, although there was no significant difference in the SST between the outer reef slope and the lagoon, the latter is an especially such shallow and closed lagoon environment, its monthly mean temperatures should be higher than that of the former (Ke et al., 2016), and it has more extreme thermal and light environments, which may limit Symbiodiniaceae reproduction and possibly reduce their density. It may even lead to coral bleaching (Hoegh-Guldberg, 1999; Fitt et al., 2000; Grimsditch et al., 2010). Indeed, we also observed several bleached corals in the lagoon, but none in the outer reef slope. Nevertheless, specific information regarding the monthly mean temperatures and solar radiation of the outer reef slopes and lagoons in the HA is not available. Thus, further research is required to confirm these factors and their influence on geomorphologically controlled variations of SD in this region.



**Fig. 3.** Geomorphological differences in Symbiodiniaceae densities (SDs) of corals in the Huangyan Atoll. All error bars are standard errors, and letters above bars (e.g., a, b, and c) denote statistical differences among coral genera in regards to SDs (Student–Newman–Keuls test,  $p < 0.05$ ).



**Fig. 4.** Spatial differences of Symbiodiniaceae densities (SDs) among the Huangyan Atoll and several coral reefs in the South China Sea. Data on SDs of other coral reefs were acquired from Qin’s studies. All error bars are standard errors, and letters above bars (e.g., a, b, and c) denote statistical differences between the indicated coral genera among the four reefs (Student–Newman–Keuls test,  $P < 0.05$ ).

**4.3. Spatial differences of SDs in the SCS and the potential of the HA to act as a refuge**

The present results suggest that corals in the HA have a high level of SDs, which is significantly higher than that of the Nansha Islands in the south and the Xisha Islands in the north. In addition, it is worth nothing that although the SDs of the Sanya in higher latitude are higher than those of in the HA, there is no obvious difference.

According to the research of Qin et al. (2019a), the variation in SDs of corals among coral reefs in the SCS was mainly related to SST and

levels of nutrients. The results showed that relatively low SST and high nutrient levels in the high-latitude reefs contribute to high SDs. In contrast, the high SST and the poor nutrient levels in the low-latitude reefs limit Symbiodiniaceae reproduction and reduce their density, thus showing a trend of increase with latitude. Similarly, our results support this finding. The average annual SST of the HA in 2015 and chlorophyll *a* concentration was just between Xisha Islands and Sanya (Ke et al., 2016, 2018; Qin et al., 2019a, 2019b). Therefore, the SDs in the HA is significantly higher than those in Nansha and Xisha Islands.

However, it is worth nothing that the SD is significantly higher in the

HA than in the Xisha Islands with the similar thermal stress, and there is no significant difference between with the Sanya in higher latitude. Therefore, we suggest that the corals of the HA may be the same as the Sanya, with less thermal stress. Wind stress in Summer induces the water northward in the HA. However, when the northern eddy is strong enough, it may also pass over the HA, causing local upwelling (Fang et al., 1998; Hu et al., 2000; Xie et al., 2003). This may reduce the impact of thermal anomalies, as coral reefs with upwelling areas have been shown to be less susceptible to heat bleaching (Nakamura, 2010; Osinga et al., 2017). During our investigation, the HA was in the middle stage of an extremely high SST event, but the corals did not appear to bleach widely despite the SST exceeding 30.3 °C (the average SST of large-scale bleaching of 47 coral reefs in 1998) (Lough, 2000). This tolerance of corals also demonstrates our points. Indeed, analysis of the Degree Heating Week data of the study region further reveal that the cumulative thermal stress was insufficient to drive bleaching on its own at this time (Fig. S4) (Strong et al., 2011). Most notably, the SST in the summer of 2015 was not the highest that has been recorded, the SST in the summers of 2010, 2013 and 2014 were higher than that in 2015. If widespread coral bleaching occurred in 2015, theoretically, more severe coral bleaching should have occurred two years previously, but no large-scale bleaching of corals has been observed in the HA. In contrast to the HA, coral bleaching occurred in Nansha Islands (SST: ~23 °C) and in Sanya, Hainan Island (SST: ~25 °C) with lower SST (Gong et al., 2019). Consequently, different environmental conditions among reefs in the SCS, such as SST, nutrients level, and local environment, caused the variation in SDs. The environmental factors of the HA may mitigate the negative effects of temperature anomalies and contribute to the thermal resistance and faster recovery of reef-building corals after periods of thermal stress.

A growing number of studies demonstrate that potential coral refuges are identifiable through specific features, such as lack of thermal anomalies, higher thermal tolerance, and higher coral species diversity (Yamano et al., 2011; Cacciapaglia and van Woeseik, 2015; Osman et al., 2017; Tkachenko and Soong, 2017). For example, the reefs of the Dongsha Atoll, a refuge for reef-building corals in the northern SCS, have developed resilience and resistance to global climate change (Tkachenko and Soong, 2017). Similarly, reef-building corals in the thermal refuge of the northern Red Sea exhibit higher thermal tolerance (Osman et al., 2017). Our results also demonstrate a similar potential in the HA, where the corals have higher SDs and thermal tolerance. In addition, the HA may have a unique local upwelling that reduces their coral exposure to thermal stress. In the light of these results, the HA may serve as a potential refuge for reef-building corals in the SCS under global warming.

However, several studies have shown that the HA is currently under severe pressure from overfishing, which is likely to result in a significant decline in live coral coverage and SDs (Ke et al., 2016; Zhao et al., 2016). This suggests that the function of the refuge in the HA is currently compromised. Overall, although this atoll could potentially serve as a refuge for corals from future global warming, severe anthropogenic disturbance may largely compromise this function. Taken together, these analyses indicate that it is critical to strengthen the surveillance of coral reef ecosystems and conduct further research on the ecological integrity and biodiversity of coral reefs in the HA.

## 5. Conclusions

The analysis results of the SDs in corals showed that there were significant intergeneric and geomorphological differences in the HA. Specifically, SDs in massive corals were significantly higher than those in encrusting and branching corals, which may reflect a greater thermal tolerance of the former. In addition, Geomorph analysis showed that the SDs of corals in the outer reef slope were higher than in the lagoon. Environmental conditions, such as hydrodynamic conditions and SST were likely the main influencing factors. Most notably, the SDs of corals

in HA were at a high level compared with that in reefs of different latitudes in the SCS, indicating that their corals have strong thermal tolerance. Further analysis showed that there may be local upwelling in the HA, which can reduce the thermal exposure of corals. These results suggest that the HA has the potential to serve as a coral refuge against future global warming. However, increasing human disturbance may limit this function.

## CRedit authorship contribution statement

This manuscript has not been submitted to other journals. All authors have seen the manuscript and agree to its submission to *Marine Pollution Bulletin*. The authors declare no competing financial interests.

## Declaration of competing interest

The authors declare that there are no competing financial interests to the research.

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## Appendix A. Supplementary data

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