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# Spatial variations in the trophic status of *Favia palauensis* corals in the South China Sea: Insights into their different adaptabilities under contrasting environmental conditions

Shendong XU<sup>1,2,3†</sup>, Zhinan ZHANG<sup>1†</sup>, Kefu YU<sup>1,2,3\*</sup>, Xueyong HUANG<sup>1,3</sup>, Hanji CHEN<sup>1</sup>, Zhenjun QIN<sup>1</sup> & Risheng LIANG<sup>1</sup>

<sup>1</sup> Guangxi Laboratory on the Study of Coral Reefs in the South China Sea; Coral Reef Research Centre of China; School of Marine Sciences, Guangxi University, Nanning 530004, China;

<sup>2</sup> Laboratory for Marine Geology, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266061, China;

<sup>3</sup> Southern Marine Science and Engineering Guangdong Laboratory (Zhuhai), Zhuhai 519000, China

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**Abstract** Scleractinian corals exhibit a dual trophic pattern of autotrophic photosynthesis and heterotrophic predation. However, whether corals can adjust their trophic status under contrasting environmental conditions remains unclear. In our study, 70 scleractinian corals (*Favia palauensis*) were collected from Sanya and the Xisha and Nansha Islands in the South China Sea. We measured the zooxanthellae density (ZD) and  $\delta^{13}\text{C}$  of zooxanthellae ( $\delta^{13}\text{C}_z$ ) and host tissue ( $\delta^{13}\text{C}_h$ ) and analyzed the difference between  $\delta^{13}\text{C}_h$  and  $\delta^{13}\text{C}_z$  (i.e.,  $\Delta^{h-z}{}^{13}\text{C}$ ). The relatively high ZD and  $\delta^{13}\text{C}_z$  values in the samples from Sanya indicate that these corals might have higher photosynthetic rates and autotrophic abilities than those from Xisha and Nansha. In contrast, the relatively low  $\delta^{13}\text{C}_h$  and  $\Delta^{h-z}{}^{13}\text{C}$  values in the samples from Xisha and Nansha suggest that these corals might have a higher heterotrophic ability than those from Sanya. In addition, we tested the coral tissue biomass and skeletal  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C}_s$ ) in the samples from Sanya and examined their correlations with  $\Delta^{h-z}{}^{13}\text{C}$ . The results showed a negative correlation, indicating that the more the organic material produced by the coral, the stronger its heterotrophic ability. Our results show that corals can adjust their trophic status under different environmental and physiological conditions, which is essential for increasing their adaptability to different environmental conditions.

**Keywords** Scleractinian corals, Symbiotic zooxanthellae density, Stable carbon isotope, Trophic status, Spatial variation, South China Sea

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## 1. Introduction

Scleractinian corals thrive in a relatively nutrient-poor, tropical marine environment and possess the capability for mixotrophy (autotrophic and heterotrophic) (Goreau et al., 1971; Risk et al., 1994; Reynaud et al., 2002; Bachar et al.,

2007; Ferrier-Pagès et al., 2018). On the one hand, scleractinian corals are hosts for photosynthetic symbiosis and rely mainly on photosynthetically derived nutrients transferred from their photosymbionts for daily metabolism (Muscatine, 1980; Nahon et al., 2013; Tremblay et al., 2012, 2015). On the other hand, corals can also be heterotrophic, as they feed on a variety of sources, including zooplankton (Houlbrèque et al., 2003), phytoplankton (Ferrier-Pagès et

† Contributed equally to this work

\* Corresponding author (email: [kefuyu@scsio.ac.cn](mailto:kefuyu@scsio.ac.cn))

al., 2011), dissolved organic compounds (Godinot et al., 2011) and suspended particulate matter (Mills et al., 2004). Heterotrophic predation provides adequate phosphorus, nitrogen and other micronutrients that are deficient in photosynthetic products (Fabricius et al., 1995; Bachar et al., 2007; Ferrier-Pagès et al., 2018). In addition, heterotrophy can improve the adaptability and resistance of corals to harsh environmental conditions (Tremblay et al., 2015, 2016), as well as contribute to coral survival and recovery from severe thermal bleaching (Grottoli et al., 2004, 2006; Krueger et al., 2018). Thus, we can further understand environmental stress adaptability, tolerance and bleaching resilience of coral by analyzing their trophic status. Laboratory experiments and *in situ* studies have shown that a coral's trophic status can be explicated by different environmental parameters, such as light availability (Falkowski et al., 1984; Muscatine et al., 1989; Grottoli and Wellington, 1999; Alamaru et al., 2009), seawater turbidity (Anthony and Fabricius, 2000; Heikoop et al., 2000; Nahon et al., 2013), nutrient status (Fox et al., 2018) and particulate matter concentration (Ferrier-Pagès et al., 2011). However, the results of these studies lacked comparative analysis of trophic status and coral physiological indicators, such as symbiotic zooxanthellae density (ZD). In addition, these studies mainly focused on a single factor at small spatial scales (e.g., depth, islands and archipelagoes), while few studies have investigated the spatial variations in coral trophic flexibility under contrasting environmental conditions over a large spatial scale.

The South China Sea (SCS) (4°N–21°N, 105°E–118°E) covers an area of approximately  $3.5 \times 10^6 \text{ km}^2$ , which includes subtropical and tropical regions, where corals are widely distributed (Yu, 2012). There are significant differences in the environmental conditions between the northern, central and southern SCS. Coral reefs in the northern SCS are seriously affected by human activities such as tourism, overfishing, coastal construction and oil pollution (Zhao et al., 2008; Dou et al., 2015; Wang et al., 2016; Xu et al., 2018), which lead to turbid and eutrophic seawater environmental conditions (Zhao et al., 2012, 2013). Environmental conditions of coral reefs in the central and southern SCS are characterized by relatively low nutrient levels, high transparency and sea surface temperature (SST) compared with those in the northern SCS (Qin et al., 2019). Coral reefs in the central and southern SCS are less affected by human activities but are more likely to be threatened by natural conditions, such as elevated seawater temperatures and excessive light/ultraviolet exposure. However, whether there are differences in the trophic status/flexibility of corals among the northern, central and southern SCS is not yet clear. The SCS provides an excellent natural laboratory to study the spatial variations and possible controlling factors of coral trophic status under contrasting environmental conditions over a large spatial scale. Thus, the potential

impact of trophic status on the environmental stress adaptability, tolerance and bleaching resilience of coral were analyzed.

Carbon isotopic compositions ( $\delta^{13}\text{C}$ ) have been proven to be a good indicator of trophic status and metabolic function (DeNiro and Epstein, 1978; Alamaru et al., 2009; Maier et al., 2010; Ferrier-Pagès and Leal, 2019). The separate analysis of  $\delta^{13}\text{C}$  of symbiotic zooxanthellae ( $\delta^{13}\text{C}_z$ ) and coral host tissue ( $\delta^{13}\text{C}_h$ ) can specifically indicate if fixed carbon is received from autotrophic or heterotrophic metabolism (Muscatine et al., 1989; Rodrigues and Grottoli, 2006; Maier et al., 2010; Seemann, 2013; Nahon et al., 2013). The  $\delta^{13}\text{C}_z$  and  $\delta^{13}\text{C}_h$  of coral are affected by physiological indicators and environmental factors (Williams et al., 2018). For instance, changes in the available light intensity or nutrient resources can alter coral ZD and photosynthetic rates, thereby altering the pattern of carbon fractionation (Marubini and Davies, 1996; Hoegh-Guldberg, 1999; Tremblay et al., 2014). Decreased rates of photosynthetic fractionation cause  $\delta^{13}\text{C}_z$  and  $\delta^{13}\text{C}_h$  values to decrease (Muscatine et al., 1989; Swart et al., 2005a). In addition, high seawater nutrient concentrations may increase heterotrophic nutrition, leading to a reduction in  $\delta^{13}\text{C}_h$  values (Rodrigues and Grottoli, 2006; Nahon et al., 2013). The difference between  $\delta^{13}\text{C}_h$  and  $\delta^{13}\text{C}_z$  (i.e.,  $\Delta^{13}\text{C}$ ) is indicative of the relative contributions of autotrophic photosynthesis and heterotrophic predation to fixed carbon, which prompted us to disentangle the relative effects of photosynthetic fractionation and the incorporation of heterotrophic carbon (Risk et al., 1994; Reynaud et al., 2002; Fox et al., 2018; Ferrier-Pagès and Leal, 2019). Theoretically,  $\delta^{13}\text{C}_h$  and  $\delta^{13}\text{C}_z$  values are similar or  $\delta^{13}\text{C}_h$  values may even be slightly higher than  $\delta^{13}\text{C}_z$  values, indicating that the contribution of heterotrophy to carbon fixation in coral polyps is very small or negligible. However, when  $\delta^{13}\text{C}$  values of coral hosts and their photosymbionts become increasingly disparate (i.e.,  $\delta^{13}\text{C}_h$  is significantly lower than  $\delta^{13}\text{C}_z$ , and the  $\Delta^{13}\text{C}$  values become more negative), the degree of heterotrophy in corals increases (Muscatine et al., 1989; Rodrigues and Grottoli, 2006). Thus,  $\delta^{13}\text{C}_z$ ,  $\delta^{13}\text{C}_h$  and  $\Delta^{13}\text{C}$  provide us with effective tools to study patterns of the trophic status (i.e., relative contributions of autotrophic and heterotrophic nutrients) of corals under the influence of different environmental conditions in the SCS.

In this study, a total of 70 samples of *Favia palauensis*, a type of scleractinian coral, were collected from Sanya and the Xisha Islands and Nansha Islands. We analyzed physiological and geochemical indexes, including ZD,  $\delta^{13}\text{C}_z$ ,  $\delta^{13}\text{C}_h$  and  $\Delta^{13}\text{C}$ , of these samples. In addition, we also analyzed the coral tissue biomass and skeletal  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C}_s$ ) of samples ( $n=23$ ) from the Sanya fringing reefs. We also collected and analyzed environmental parameters, such as seawater nutrient levels, turbidity, transparency and SST, in three coral reef regions (CRRs). The purpose of this study is (1) to

investigate the spatial variations and possible controlling factors for the trophic status of coral under contrasting environmental conditions over a large spatial scale in the SCS and (2) to explore the correlation between coral trophic status and the amount of organic material produced by symbiotic zooxanthellae and coral hosts. Our results provide insights into further understanding coral adaptive mechanisms, which lead to the different ecological phenomena observed in the field, such as variations in live coral cover and degradation rate under different environmental conditions.

## 2. Materials and methods

### 2.1 Study sites and coral sampling

Our study was conducted in three CRRs in the SCS: Sanya, Xisha Islands and Nansha Islands (Figure 1 and Appendix Table S1, <https://link.springer.com>). Sanya is a typical fringing reef located in the northern SCS at relatively high latitudes. The Xisha Islands are located in the central SCS and include numerous atolls and island reefs (Wang et al., 2011). The relatively low-latitude Nansha Islands are located in the southernmost part of the SCS and include more than 25 atolls and/or island reefs (Qin et al., 2019). Both the Xisha and Nansha Islands are relatively less affected by anthropogenic activities because they are far removed from the surrounding populated mainland (Wang et al., 2011; Zhu et al., 2016).

A total of 70 coral samples of *Favia palauensis* were collected during May–August 2015 from the Sanya fringing reefs (18°13'N, 109°29'E;  $n=23$ ), Xisha Islands (16°N–17°N, 111°E–113°E;  $n=27$ ) and Nansha Islands (9°N–10°N, 115°E–116°E;  $n=20$ ) at depths of ~2–4 m. All sample fragments (20–50 cm<sup>2</sup>) were randomly collected from each healthy coral group and immediately preserved at –20°C until experimental analysis.

### 2.2 Experimental processing methods and geochemical analyses

#### 2.2.1 Determination of ZD

The samples were sealed in a container, and coral tissues were separated from the coral skeleton with a Waterpik containing filtered seawater (0.45 μm). The volume of coral tissue homogenate was measured with a graduated cylinder (Xu et al., 2017). Four equal parts (3 mL) were extracted from tissue homogenates and centrifuged. The supernatant was slowly removed, and the remaining algae were fixed with 1 mL 5% formaldehyde for 2–4 h and then stored at 0°C for microscopic observation. The number of zooxanthellae was calculated by replicate ( $n=8$ ) hemocytometer counts and converted into the number of zooxanthellae contained in the total slurry volume. The surface area of coral was calculated

according to the relationship between the weight and area of aluminum foil. ZD was obtained by the number of zooxanthellae and the area of the coral sample (Johannes and Wiebe, 1970; Fagoonee et al., 1999; Sawall et al., 2014).

#### 2.2.2 Measurement of tissue biomass

Approximately 3–6 mL of tissue slurry was dried to a constant weight in a precombusted aluminum pan at 60°C and then ashed at 500°C for 4 h in a muffle furnace. The ash-free dry weight (tissue biomass) was calculated from the difference between the dry and ash weights and standardized to surface area. The coral surface area was estimated based on the relationship between the aluminum foil weight and area (Fitt et al., 2000; Schoepf et al., 2015).

#### 2.2.3 Separation of zooxanthellae and host tissue

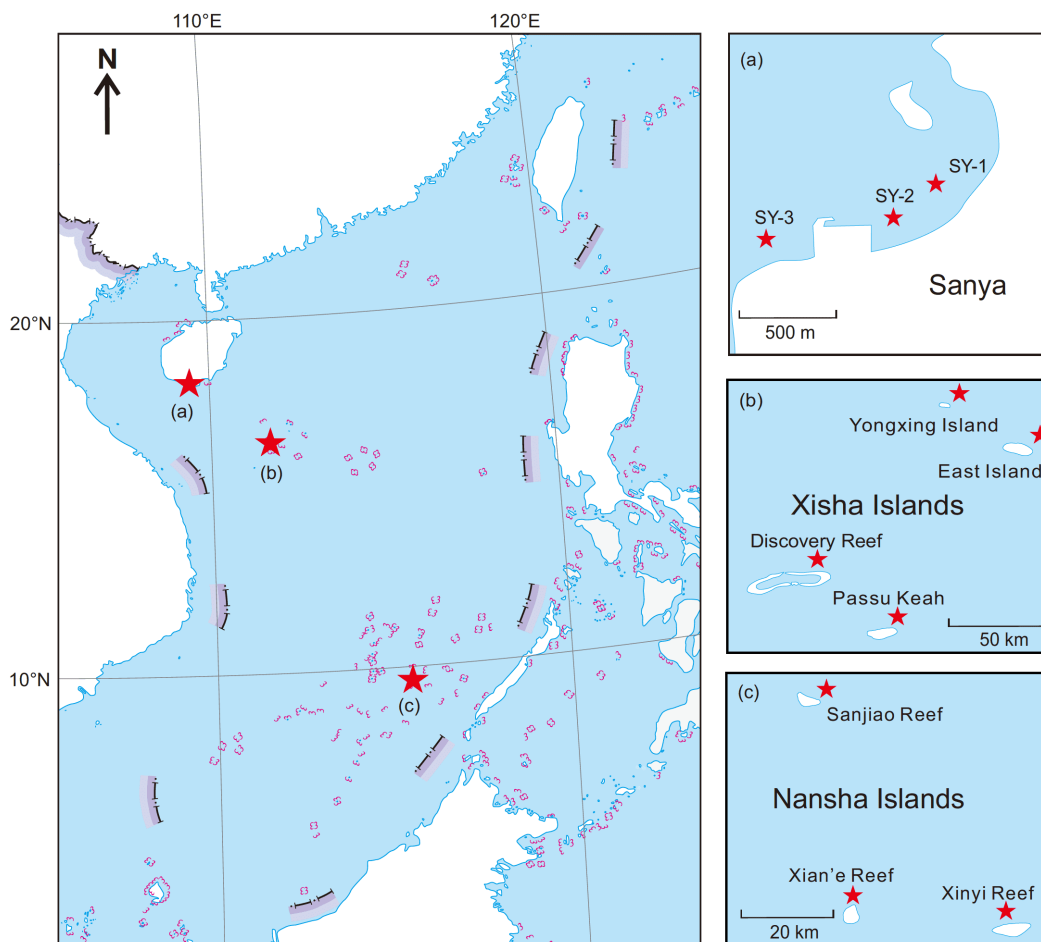
After the ZD and tissue biomass were determined, the remaining tissue slurry was homogenized and separated into zooxanthellae and host tissue via centrifugation (1500 r min<sup>-1</sup>; 10 min). The supernatant (host tissue) was slowly poured into a centrifuge tube and centrifuged. The centrifugation process was repeated five times ensuring that the zooxanthellae could not be detected in the supernatant under a microscope. The supernatant (host tissue) was filtered onto a Whatman GF/F filter (47 mm, 0.7 μm), and the filter membranes were collected in a sealed bag and frozen for subsequent isotopic analysis (Papina et al., 2003; Treignier et al., 2008). The zooxanthellae pellets were decalcified by adding 0.5 mL HCl (1 N) to the samples. When the slurry stopped bubbling, all samples were resuspended in filtered seawater, purified twice by centrifugation, and then collected with a sample bag. Both the filter membrane (host tissue) and zooxanthellae pellets were washed in diluted HCl to remove any adhered carbonate material, washed in distilled water and dried in an oven for 24 h (40°C) for subsequent δ<sup>13</sup>C isotopic analysis (Swart et al., 2005b; Alamaru et al., 2009; Seemann, 2013).

#### 2.2.4 Treatment of the coral skeleton

The coral skeleton was dried in an oven for at least 24 h. Approximately 0.5–1 mg of powdered calcium carbonate was gently scraped from the coral skeleton using a surgical blade. Before collecting samples, the surface of the coral skeleton was milled to remove the upper 1 mm. The powdered samples were wrapped in weighing paper and stored for δ<sup>13</sup>C isotopic analysis.

#### 2.2.5 Analysis of stable isotopes

δ<sup>13</sup>C<sub>h</sub> and δ<sup>13</sup>C<sub>z</sub> were analyzed with an elemental analysis-isotope ratio mass spectrometry (EA-IRMS) system with a FLASH 1112 series elemental analyzer interfaced with a DELTA A<sup>plus</sup> XL mass spectrometer. Tests were completed in the State Key Laboratory of Organic Geochemistry,



**Figure 1** The study area and sampling sites in the South China Sea (The geographical base map of China was downloaded from <http://bzdt.ch.mnr.gov.cn/>). (a) Sampling point map of Sanya (red pentagram); (b) sampling point map of the Xisha Islands (red pentagram); (c) sampling point map of the Nansha Islands (red pentagram). The geographical base map of Sanya, the Xisha Islands and Nansha Islands was downloaded from <https://map.tianditu.gov.cn/>.

Guangzhou Institute of Geochemistry, Chinese Academy of Sciences (GIGCAS). To monitor the instrumental stability and measurement accuracy of the IRMS system, an organic analytical standard consisting of a homogenous batch of protein (Casien) standards with known  $\delta^{13}\text{C}$  values (i.e.,  $\delta^{13}\text{C}_{\text{V-PDB}} = -26.98 \pm 0.13\text{‰}$ ) was inserted between every 10 samples throughout the test, and multiple measurements of this standard yielded a standard deviation (SD) of 0.3‰ for  $\delta^{13}\text{C}$ . Each sample was analyzed at least twice, and the average value was expressed using  $\sigma \leq 0.2\text{‰}$ . The  $\delta^{13}\text{C}$  values of zooxanthellae and host tissue are reported relative to international Vienna-Peedee Belemnite Limestone standards (V-PDB) (Alamaru et al., 2009).

$\delta^{13}\text{C}_s$  values were tested using a Finnigan MAT-253 stable mass spectrometer connected to a Fairbanks carbonate preparation device at the Coral Reef Research Center of China (School of Marine Sciences, Guangxi University). In an automatic carbonate device, powdered samples were reacted with 100%  $\text{H}_3\text{PO}_4$  at 75°C to extract  $\text{CO}_2$ . An SD of 0.03‰ for  $\delta^{13}\text{C}$  was determined by multiple measurements of the Chinese national standard GBW04405. All samples were

tested twice to ensure that the difference between the two measurements was within the analytical error range. The  $\delta^{13}\text{C}$  values were reported in the per mil (‰) convention relative to the V-PDB standard (Deng et al., 2013; Xu et al., 2018).

### 2.3 Collection of environmental parameters

The SST and sea surface salinity (SSS) data for the three CRRs were downloaded from the National Oceanic and Atmospheric Administration, Physical Sciences Division, Gridded Climate Datasets (NOAA, PSD, Gridded Climate Datasets, <https://www.esrl.noaa.gov/psd/data/gridded/>). Remote sensing data of particulate organic carbon (POC) and chlorophyll (Chl) *a* concentration of surface seawater were collected from the National Aeronautics and Space Administration (NASA, <https://giovanni.gsfc.nasa.gov>). Other *in situ* seawater parameters, such as SST, pH, turbidity and transparency, as well as laboratory measured parameters, such as dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP), for the three CRRs have been re-

ported in a previous study. For more information, please refer to Qin et al. (2019).

## 2.4 Statistical analysis

We used one-way factorial analysis of variance (ANOVA) to test the spatial variations in ZD,  $\delta^{13}C_z$ ,  $\delta^{13}C_h$  and  $\Delta^{h-z} 13C$ . Levene's test and Shapiro-Wilk's test were used to verify the assumptions of homoscedasticity and normality. The ZD data were log transformed to meet homoscedasticity. In addition, we used a Student-Newman-Keuls test for post hoc multiple comparisons of the ANOVA results. All data are expressed as the mean±SD. In addition, the correlations between the ZD and environmental parameters and their respective influences on the coral stable carbon isotope values were analyzed using Pearson's correlation.

## 3. Results

### 3.1 Coral physiological parameters

The densities of zooxanthellae were significantly different among the samples from Sanya, the Xisha Islands and the Nansha Islands (one-way ANOVA,  $F=26.5$ ,  $p<0.001$ ; Table 1). Specifically, the mean ZD values of samples from Sanya, the Xisha Islands and Nansha Islands are  $(3.02\pm1.09)\times10^6$ ,  $(1.98\pm0.72)\times10^6$ , and  $(1.3\pm0.38)\times10^6$  cells  $cm^{-2}$ , respectively, as shown in Figure 2 and Appendix Tables S2, S3. The results show that ZD increases with increasing latitude. In addition, the tissue biomass of coral samples collected in Sanya varied from 9.45 to 27.54  $mg\ cm^{-2}$ , with an average value of  $18.32\pm5.39\ mg\ cm^{-2}$ , as shown in Appendix Table S4.

### 3.2 Carbon isotopic composition

#### 3.2.1 $\delta^{13}C_z$ , $\delta^{13}C_h$ and $\delta^{13}C_s$ values

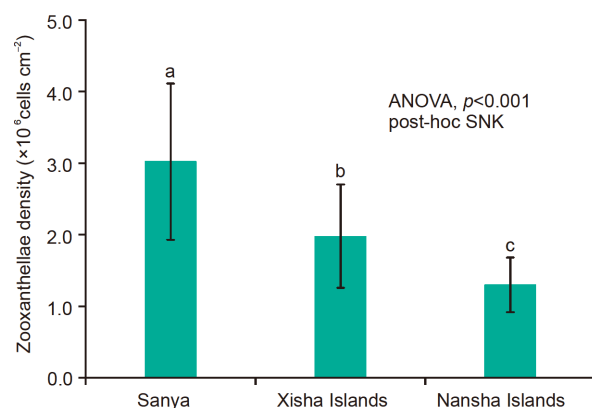
$\delta^{13}C_z$  and  $\delta^{13}C_h$  values show significant spatial variations (one-way ANOVA,  $\delta^{13}C_z$ :  $F=3.6$ ,  $p<0.05$ ;  $\delta^{13}C_h$ :  $F=32.8$ ,  $p<0.001$ ; Table 1). The mean  $\delta^{13}C_z$  values are  $-12.52\pm1.09\text{‰}$ ,  $-13.27\pm1.42\text{‰}$ , and  $-13.45\pm1.06\text{‰}$ , and the mean  $\delta^{13}C_h$  values are  $-13.27\pm0.95\text{‰}$ ,  $-15.34\pm1.1\text{‰}$ , and  $-15.63\pm1.16\text{‰}$  in the samples from Sanya, the Xisha Islands and the Nansha Islands, respectively (Figure 3a and 3b, Appendix Tables S2, S3). Thus, coral zooxanthellae and host tissue are relatively most  $^{13}C$ -enriched in Sanya compared with those in the Xisha and Nansha Islands. In addition, the  $\delta^{13}C_s$  of coral samples collected from Sanya varied from  $-2.46\text{‰}$  to  $-0.40\text{‰}$ , with an average value of  $-1.4\pm0.56\text{‰}$ , as shown in Figure 6 and Appendix Table S4.

#### 3.2.2 $\Delta^{h-z} 13C$ values

$\Delta^{h-z} 13C$  is diagnostic of the relative contribution of photo-

**Table 1** One-way ANOVA testing the spatial effect on ZD and isotopic composition of corals ( $\delta^{13}C_z$ ,  $\delta^{13}C_h$  and  $\Delta^{h-z} 13C$ )

Parameters	Value	
ZD	<i>F</i>	26.5
	<i>p</i>	<0.001
$\delta^{13}C_z$	<i>F</i>	3.6
	<i>p</i>	<0.05
$\delta^{13}C_h$	<i>F</i>	32.8
	<i>p</i>	<0.001
$\Delta^{h-z} 13C$	<i>F</i>	8.9
	<i>p</i>	<0.001

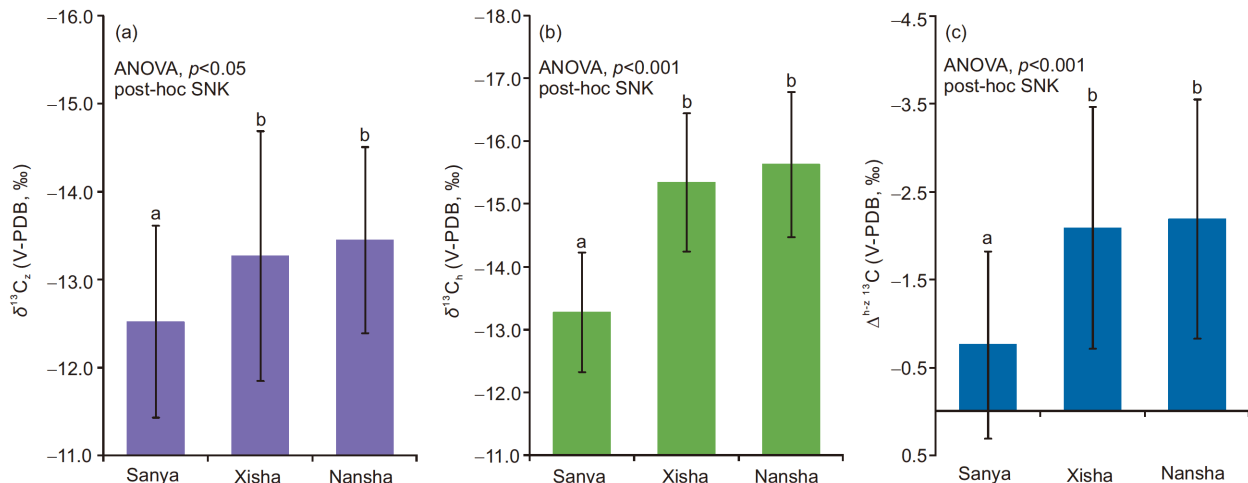


**Figure 2** The zooxanthellae density average values are expressed as the mean±SD in the samples from coral reefs in Sanya, the Xisha Islands and the Nansha Islands. a–c indicate posthoc multiple comparisons of ZD among sampling sites.

synthetically fixed carbon and heterotrophically acquired carbon to coral polyps (Muscatine et al., 1989; Reynaud et al., 2002; Rodrigues and Grottoli, 2006). The  $\Delta^{h-z} 13C$  values also show obvious spatial variations (one-way ANOVA,  $F=8.9$ ,  $p<0.001$ ; Table 1). The mean  $\Delta^{h-z} 13C$  values are  $-0.75\pm1.06\text{‰}$ ,  $-2.08\pm1.37\text{‰}$ , and  $-2.18\pm1.36\text{‰}$  in samples from Sanya and the Xisha and Nansha Islands, respectively, as shown in Figure 3c and Appendix Table S2. Obviously, coral  $\Delta^{h-z} 13C$  values in the Xisha and Nansha Islands are relatively lower than those in Sanya.

### 3.3 Environmental and water parameters

Environmental parameters varied significantly among Sanya and the Xisha and Nansha Islands (Table 2 and Appendix Tables S3, S5). Overall, SST increases gradually with decreasing latitude. Both SSTs measured *in situ* and downloaded from the website are lower in Sanya than in the Xisha and Nansha Islands (Table 2). In addition, at the Nansha Islands, both *in situ* SST and May–August average SST in 2015 were higher than 30°C (Table 2 and Appendix Table S5). Nutrient (i.e., DIN and SRP) concentrations are higher



**Figure 3** The  $\delta^{13}\text{C}_z$ ,  $\delta^{13}\text{C}_h$  and  $\Delta^{13}\text{C}$  values are expressed as the mean $\pm$ SD in the samples from coral reefs in Sanya, the Xisha Islands and the Nansha Islands. (a) The average  $\delta^{13}\text{C}_z$  values; (b) the average  $\delta^{13}\text{C}_h$  values; (c) the average  $\Delta^{13}\text{C}$  values in Sanya, the Xisha Islands and Nansha Islands coral reefs. The a and b indicate post-hoc multiple comparisons the coral isotope values among sampling sites.

**Table 2** Environmental parameters of Sanya and the Xisha and Nansha Islands in the SCS

Parameters	Sanya	Xisha Islands	Nansha Islands
Annual mean SST ( $^{\circ}\text{C}$ )	26.38 $\pm$ 0.36	27.56 $\pm$ 0.33	28.62 $\pm$ 0.30
May–August mean SST ( $^{\circ}\text{C}$ )	28.99 $\pm$ 0.39	29.30 $\pm$ 0.34	29.45 $\pm$ 0.37
Annual mean SSS (‰)	33.60 $\pm$ 0.15	33.64 $\pm$ 0.20	33.28 $\pm$ 0.22
May–August mean SSS (‰)	33.52 $\pm$ 0.15	33.65 $\pm$ 0.23	33.38 $\pm$ 0.23
POC ( $\text{mg m}^{-3}$ )	135.6 $\pm$ 27	<45.4 $\pm$ 1.18	<51.7 $\pm$ 2.02
Chl <i>a</i> ( $\text{mg m}^{-3}$ )	0.5 $\pm$ 0.11	0.1 $\pm$ 0.07	0.13 $\pm$ 0.09
<i>In-situ</i> turbidity (NTU)	1.0–1.2	0.2–0.38	0.1–0.23
<i>In-situ</i> transparency (m)	4.6	17.7	24.4
<i>In-situ</i> SST ( $^{\circ}\text{C}$ )	28.8	29.8	30.6
<i>In-situ</i> pH	8.18	8.24	8.21
DIN ( $\mu\text{mol L}^{-1}$ )	2.94	1.31	1.37
SRP ( $\mu\text{mol L}^{-1}$ )	0.49	0.08	0.05

at Sanya than at the Xisha and Nansha Islands. In addition, Sanya has higher Chl *a* and POC concentrations and turbidity than the Xisha and Nansha Islands (Table 2). In contrast, seawater transparency at the Sanya coral reefs is much lower than that at the Xisha and Nansha Islands (Table 2). In our study, there were no significant differences in SSS and pH values among the three CRRs.

### 3.4 Correlations among ZD, $\delta^{13}\text{C}_z$ , $\delta^{13}\text{C}_h$ and environmental parameters

#### 3.4.1 Correlations between ZD and environmental parameters

Spatial variations in ZD are closely linked with different environmental conditions among the three CRRs, such as seawater transparency, nutrient levels and SST. Pearson correlation (2-tailed) analysis shows that ZD is significantly

negatively correlated with seawater transparency ( $r=-0.656$ ,  $p<0.001$ ,  $n=70$ ) (Table 3). In addition, ZD was also significantly negatively correlated with SST, regardless of whether the annual mean SST ( $r=-0.655$ ,  $p<0.001$ ,  $n=70$ ) or the May–August mean SST ( $r=-0.655$ ,  $p<0.001$ ,  $n=70$ ) was used (Table 3). In contrast, ZD is positively correlated with seawater nutrients, such as DIN ( $r=0.592$ ,  $p<0.001$ ,  $n=70$ ) and SRP ( $r=0.616$ ,  $p<0.001$ ,  $n=70$ ) (Table 3). Some other factors, such as SSS and pH, seem to have a weak correlation with ZD.

#### 3.4.2 Correlations between $\delta^{13}\text{C}_z$ and ZD and environmental parameters

Spatial variations in  $\delta^{13}\text{C}_z$  values could be explained by the photosynthetic rate of symbiotic zooxanthellae. ZD is an important factor influencing photosynthetic rate (Porter et al., 1989; Hoegh-Guldberg, 1999; Titlyanov et al., 2000;

**Table 3** Correlations between ZD and environmental parameters for all samples<sup>a)</sup>

Parameters	Pearson correlation	Sig. (2-tailed)	N
Annual mean SST (°C)	-0.655**	0	70
May–August mean SST (°C)	-0.655**	0	70
Annual mean SSS (‰)	0.456**	0	70
May–August mean SSS (‰)	0.227	0.059	70
pH	-0.399**	0.001	70
DIN (μmol L <sup>-1</sup> )	0.592**	0	70
SRP (μmol L <sup>-1</sup> )	0.616**	0	70
Chl <i>a</i> (mg m <sup>-3</sup> )	0.582**	0	70
Turbidity (NTU)	0.629**	0	70
Transparency (m)	-0.656**	0	70

a) \*\* Correlation is significant at the 0.01 level (2-tailed)

Alamaru et al., 2009; Xu et al., 2020). We analyzed the correlation between ZD and  $\delta^{13}C_z$  of each coral sample from the three coral reefs, and the results showed that ZD and  $\delta^{13}C_z$  were positively correlated, as shown in Figure 4. In addition, previous studies have shown that turbidity and transparency may influence photosynthetic rate by affecting ZD (Hallock and Schlager, 1986; Anthony, 2000; Anthony and Fabricius, 2000). Pearson correlation analysis showed that  $\delta^{13}C_z$  is significantly positively correlated with turbidity ( $r=0.312, p<0.01, n=70$ ; Table 4) and negatively correlated with transparency ( $r=-0.309, p<0.01, n=70$ ; Table 4).

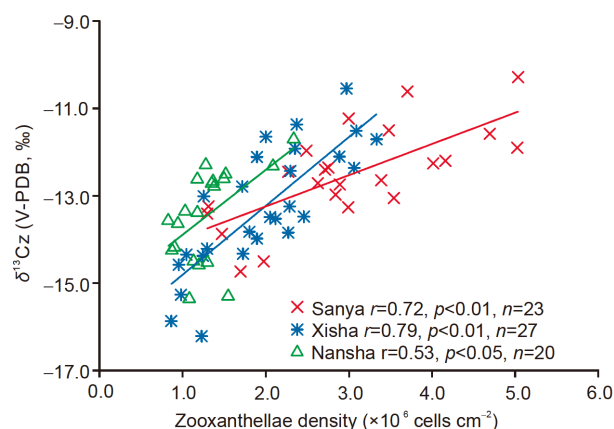
### 3.4.3 Correlations between $\delta^{13}C_h$ , $\Delta^{h-z} 13C$ and environmental parameters

Seawater Chl *a* and POC concentrations represent the relative amount of available heterotrophic food sources (Rodrigues and Grottoli, 2006; Nahon et al., 2013). Both  $\delta^{13}C_h$  and  $\Delta^{h-z} 13C$  should be relatively negative when corals take up more Chl *a* and POC as heterotrophic sources (Muscatine et al., 1989; Yin et al., 2014). However, our results show that both  $\delta^{13}C_h$  and  $\Delta^{h-z} 13C$  are positively correlated with Chl *a* ( $\delta^{13}C_h: r=0.692$  and  $\Delta^{h-z} 13C: r=0.455, p<0.001, n=70$ ), POC concentration ( $\delta^{13}C_h: r=0.693$  and  $\Delta^{h-z} 13C: r=0.455, p<0.001, n=70$ ) and turbidity ( $\delta^{13}C_h: r=0.703$  and  $\Delta^{h-z} 13C: r=0.458, p<0.001, n=70$ ) (Table 5). In contrast,  $\delta^{13}C_h$  and  $\Delta^{h-z} 13C$  are negatively correlated with the factors that may affect coral ZD, such as SST and transparency (Table 5).

## 4. Discussion

### 4.1 Spatial variations and controlling factors of ZD

Numerous studies have shown that ZD is affected by local environmental factors, such as SST, light intensity, nutrients, and salinity (e.g., Hoegh-Guldberg and Smith, 1989; Hoegh-Guldberg, 1994; Sunagawa et al., 2008; Sawall et al., 2011; Ladrìere et al., 2014; Muller-Parker et al., 2015). Seawater



**Figure 4** Correlations between zooxanthellae density and  $\delta^{13}C_z$  values of each coral sample from the three coral reefs.

**Table 4** Correlations between  $\delta^{13}C_z$  and environmental parameters for all samples<sup>a)</sup>

Parameters	Pearson correlation	Sig. (2-tailed)	N
Turbidity (NTU)	0.312**	0.008	70
Transparency (m)	-0.309**	0.009	70
DIN (μmol L <sup>-1</sup> )	0.306*	0.01	70
SRP (μmol L <sup>-1</sup> )	0.311**	0.009	70

a) \*\* Correlation is significant at the 0.01 level (2-tailed). \* Correlation is significant at the 0.05 level (2-tailed).

transparency directly affects the amount of sunlight available for zooxanthellae photosynthesis. Theoretically, corals living in areas with high seawater transparency may be more vulnerable to high light/ultraviolet light (Qin et al., 2019). Excessive light/ultraviolet light could hinder electron transfer in the photosynthetic system or lead to destruction of protein and consequently increase the amount of harmful reactive oxygen species (Lesser, 1996; Bhagooli and Hidaka, 2004), which may result in the discharge and loss of the symbiotic zooxanthellae (Hoegh-Guldberg, 1999; Yentsch et al., 2002;



**Table 5** Correlation between  $\delta^{13}\text{C}_h$ ,  $\Delta^{h-z}^{13}\text{C}$  and environmental parameters and ZD for all samples<sup>a)</sup>

Parameters	$\delta^{13}\text{C}_h$			$\Delta^{h-z}^{13}\text{C}$		
	Pearson correlation	Sig. (2-tailed)	<i>N</i>	Pearson correlation	Sig. (2-tailed)	<i>N</i>
Chl <i>a</i> (mg m <sup>-3</sup> )	0.692**	0	70	0.455**	0	70
POC (mg m <sup>-3</sup> )	0.693**	0	70	0.455**	0	70
Turbidity (NTU)	0.703**	0	70	0.458**	0	70
DIN (μmol L <sup>-1</sup> )	0.696**	0	70	0.457**	0	70
SRP (μmol L <sup>-1</sup> )	0.702**	0	70	0.459**	0	70
Transparency (m)	-0.683**	0	70	-0.440**	0	70
Annual mean SST (°C)	-0.648**	0	70	-0.413**	0	70
May–August mean SST (°C)	-0.686**	0	70	-0.442**	0	70

a) \*\*, Correlation is significant at the 0.01 level (2-tailed)

Venn et al., 2008; Gustafsson et al., 2014; Qin et al., 2019). Our results support these previous findings, as there is a negative correlation between the seawater transparency and ZD levels in the SCS (Table 3). The seawater transparency in the Xisha and Nansha Islands is significantly higher than that in Sanya (Table 2), which is consistent with the changes in ZD. Therefore, different seawater transparency levels may be one of the important factors leading to the spatial variations in ZD in the SCS.

In addition, corals produce destructively reactive oxygen species when SST increases. This phenomenon could also lead to the destruction and discharge of zooxanthellae, thus reducing ZD and hindering photosynthesis by zooxanthellae (e.g., Lesser, 1997; Fitt et al., 2000; Tchernov et al., 2004; Gustafsson et al., 2014; Shimokawa et al., 2014). Fujise et al. (2014) pointed out that corals in 30°C seawater actively expel damaged zooxanthellae, thus reducing their ZD. The *in situ* SST measured during sample collection in Sanya was <30°C (i.e., 28.8°C), while that in the Nansha Islands was >30°C (i.e., the average SST of the three coral reefs was 30.6°C) (Table 2). In addition, both May–August and annual mean SST were also lower at Sanya than at the Xisha and Nansha Islands; the annual mean SST at the Nansha Islands was 2.24°C higher than that at Sanya (Table 2 and Table S5). The relatively high SST makes corals at the Xisha and Nansha Islands more vulnerable to temperature stress, which could lead to a reduction in ZD. There was a negative correlation between SST and ZD, regardless of whether the annual mean ( $r=-0.655$ ,  $p<0.001$ ,  $n=70$ ) or May–August mean SST ( $r=-0.655$ ,  $p<0.001$ ,  $n=70$ ) was considered (Table 3). Thus, we consider that SST is another important factor affecting the spatial variations in ZD levels in the SCS. In addition, several studies have demonstrated that increasing nutrient concentrations are expected to accelerate zooxanthellae growth and result in high ZD levels (Hoegh-Guldberg, 1994; Li et al., 2008; Sawall et al., 2014; Muller-Parker et al., 2015; Ke et al., 2018). The DIN and SRP concentrations at Sanya were significantly higher than those

at the Xisha and Nansha Islands (Table 2). In addition, there was a positive correlation between nutrient content (i.e., DIN and SRP) and ZD (e.g., DIN:  $r=0.592$ ,  $p<0.001$ ,  $n=70$ ; and SRP:  $r=0.616$ ,  $p<0.001$ ,  $n=70$ ) (Table 3). Therefore, the effects of different seawater nutrient levels on ZD should also not be ignored in the SCS.

Overall, the spatial variations in coral ZD levels in the SCS are closely related to different environmental conditions. The relatively high seawater transparency and SST in the Xisha and Nansha Islands are not conducive to zooxanthellae reproduction and possibly reduce their density. However, the relatively high nutrient levels in the Sanya fringing reefs are conducive to zooxanthellae growth. Thus, the comprehensive effects of these factors lead to relatively high ZD levels in the Sanya fringing reefs compared with those in the Xisha and Nansha Islands.

#### 4.2 Spatial variations and controlling factors of the autotrophic ability of coral in the SCS

For scleractinian corals, photosynthesis of their zooxanthellae is generally considered the main pathway for carbon acquisition (Hoogenboom et al., 2006, 2010). Multiple studies have indicated that coral  $\delta^{13}\text{C}_z$  is regulated by the zooxanthellae photosynthetic rate (Muscatine et al., 1989; Maier et al., 2010; Nahon et al., 2013; Plass-Johnson et al., 2015). There are two principal carbon sources for symbiotic zooxanthellae photosynthesis: CO<sub>2</sub> from animal metabolism and the internal tissular bicarbonate pool (HCO<sub>3</sub><sup>-</sup>) (Muscatine et al., 1989). The  $\delta^{13}\text{C}$  value of CO<sub>2</sub> originating from animal metabolism is more negative than that originating from the internal tissular bicarbonate pool, with a value of approximately -14‰ (Nahon et al., 2013). In contrast, the  $\delta^{13}\text{C}$  of CO<sub>2</sub> resulting from the internal tissular bicarbonate pool is relatively more positive, with a value of approximately -7‰ (Rau et al., 1990). Generally, photosymbionts preferentially utilize forms of carbon that contain the light isotope <sup>12</sup>C over the heavier isotope <sup>13</sup>C during photosynthesis (McCon-

naughey, 1989a; Deng et al., 2013), which is called the metabolic isotope effect. Nevertheless, when photosynthetic rate increases, (1) photosymbionts are obliged to utilize more carbon that contains the heavier isotope  $^{13}\text{C}$ , which may lead to the reduction in carbon isotopic discrimination and an increase in  $\delta^{13}\text{C}_z$ ; and (2) photosymbionts may use an increasing fraction of carbon with a more positive  $\delta^{13}\text{C}$  value from the internal tissular bicarbonate pool (Muscatine et al., 1989; Swart et al., 2005a). Both the reduction in carbon isotopic discrimination and the increased proportion of  $\text{CO}_2$  utilized from the internal tissular bicarbonate pool could induce a relative enrichment in  $\delta^{13}\text{C}_z$  values (Rodrigues and Grottoli, 2006). In contrast, zooxanthellae will incorporate more  $^{12}\text{C}$  than  $^{13}\text{C}$ , resulting in decreased  $\delta^{13}\text{C}_z$  under the situation of decreased photosynthesis.

Therefore, any factors that affect photosynthetic rate could lead to changes in  $\delta^{13}\text{C}_z$ , such as water depth, ZD levels, turbidity and transparency. Generally, the photosynthetic rate of zooxanthellae is relatively high in shallow seawater, whereas it is relatively low in deep seawater environments with limited illumination (Land et al., 1975; Muscatine et al., 1989). In this study, all coral samples were collected at water depths from ~2–4 m. Similar sampling depths ensure that variations in  $\delta^{13}\text{C}_z$  are barely affected by different depths.

Many previous studies have shown that ZD may affect photosynthetic rate (Porter et al., 1989; Marubini and Davies, 1996; Hoegh-Guldberg, 1999; Grottoli et al., 2006), as well as  $\delta^{13}\text{C}_z$  (Swart et al., 2005a). Theoretically, the higher the ZD is, the higher the photosynthetic rate and  $\delta^{13}\text{C}_z$  values, and vice versa (Porter et al., 1989; Swart et al., 2005a; Wooldridge, 2013; Linsley et al., 2019; Xu et al., 2020). Our results show that  $\delta^{13}\text{C}_z$  was significantly positively related to ZD (Figure 4). Both the ZD and  $\delta^{13}\text{C}_z$  values of the Sanya fringing reefs were higher than those of the Xisha and Nansha Islands. Therefore, the spatial variations in  $\delta^{13}\text{C}_z$  were mainly caused by the different ZD levels and relevant photosynthetic intensities among the different coral reefs. In addition, different seawater turbidity conditions could also influence photosynthetic rate and  $\delta^{13}\text{C}_z$  by influencing the ZD level.  $\delta^{13}\text{C}_z$  was positively correlated with seawater turbidity ( $r=0.312$ ,  $p<0.01$ ,  $n=70$ ; Table 4) and negatively correlated with transparency ( $r=-0.309$ ,  $p<0.01$ ,  $n=70$ ; Table 4). Anthony and Fabricius (2000) pointed out that high turbidity indicates that more nutrients in ambient seawater are available to the zooxanthellae, leading to an increase in ZD. This condition also occurred in this study; turbidity and transparency were positively (i.e., DIN:  $r=0.988$  and SRP:  $r=0.998$ ,  $p<0.001$ ,  $n=70$ ; Table S6) and negatively (i.e., DIN:  $r=-0.928$  and SRP:  $r=-0.959$ ,  $p<0.001$ ,  $n=70$ ; Table S6) correlated with nutrients, respectively. In addition, the ZD of corals living in a high nutrient environment was relatively high (as described in Section 4.1).

Based on the above analysis, we suggest that the spatial

variation in  $\delta^{13}\text{C}_z$  in the SCS may be mainly caused by the different zooxanthellae photosynthetic rates. The zooxanthellae photosynthetic rate was closely related to the different ZD levels among the different coral reefs. Natural environmental conditions (e.g., nutrient levels, seawater turbidity and transparency) could affect photosynthesis and  $\delta^{13}\text{C}_z$  by affecting the ZD level. The relatively high ZD level and relatively high photosynthetic rate of the Sanya fringing reefs could cause corals to rely more on autotrophy to meet their daily metabolic needs compared with corals of the Xisha and Nansha Islands.

### 4.3 Spatial variations in heterotrophic predation under different environmental conditions

The difference between  $\delta^{13}\text{C}_h$  and  $\delta^{13}\text{C}_z$  ( $\Delta^{h-z}^{13}\text{C}$ ) indicates the relative contribution of heterotrophic predation and autotrophic photosynthesis to the fixation of carbon by coral polyps (Muscatine et al., 1989; Risk et al., 1994; Reynaud et al., 2002). The values of  $\delta^{13}\text{C}_h$  and  $\delta^{13}\text{C}_z$  are similar, and values of  $\delta^{13}\text{C}_h$  are even greater than those of  $\delta^{13}\text{C}_z$ , indicating that heterotrophic predation has a very small or negligible contribution to the fixation of carbon by coral polyps relative to autotrophic photosynthesis. When the degree of heterotrophic predation by the coral host increases, the  $\delta^{13}\text{C}_h$  values will decrease and approach those of  $^{13}\text{C}$ -depleted heterotrophic sources, such as zooplankton and particulate organic matter, with  $\delta^{13}\text{C}$  values ranging from  $-14\%$  to  $-25\%$ , or even more negative (Muscatine et al., 1989), which then lead to more negative  $\Delta^{h-z}^{13}\text{C}$  values. Previous studies have demonstrated that heterotrophic level varies significantly, even within conspecific coral. To the best of our knowledge, our study is the first to elaborate on the spatial variations in coral trophic status (including both autotrophic photosynthesis and heterotrophic predation) throughout the SCS by combining environmental parameters (i.e., turbidity, Chl *a* and POC concentration) with physiological indicators (i.e., ZD).

Seawater Chl *a* and POC concentrations represent the relative amount of available heterotrophic food sources, and high concentrations of Chl *a* and POC indicate that seawater turbidity may also be high (Rodrigues and Grottoli, 2006; Nahon et al., 2013). In this study, Chl *a* ( $r=0.983$ ,  $p<0.001$ ,  $n=70$ ) and POC ( $r=0.984$ ,  $p<0.001$ ,  $n=70$ ) were positively correlated with seawater turbidity (please see Appendix Table S7). Generally, the heterotrophic level of corals living in turbid seawater environments is relatively high, and the  $\delta^{13}\text{C}_h$  and  $\Delta^{h-z}^{13}\text{C}$  values are low due to the relatively large amount of heterotrophic food available (Anthony and Fabricius, 2000; Nahon et al., 2013; Plass-Johnson et al., 2015). However, the  $\delta^{13}\text{C}_h$  and  $\Delta^{h-z}^{13}\text{C}$  values of corals living in turbid environments with high Chl *a* and POC concentrations in Sanya are higher than those in the clear environments in

the Xisha and Nansha Islands (Figure 3b and 3c), indicating that the heterotrophic level of corals in Sanya is relatively low. These results suggest that spatial variations in heterotrophic levels over a large spatial scale in the SCS are not mainly controlled by the concentration of available heterotrophic food sources.

In addition, we found that  $\delta^{13}\text{C}_h$  and  $\Delta^{h-z}^{13}\text{C}$  values were negatively correlated with SST and positively correlated with nutrient content (i.e., DIN and SRP) (Table 5). As discussed in Section 4.1, SST and nutrient levels could significantly affect ZD levels in the SCS. One possible explanation is that these factors could influence the heterotrophic levels of coral by affecting their ZD levels. In the SCS, ZD levels in the Sanya fringing reefs are significantly higher than those in the Xisha and Nansha coral reefs (Figure 2). The reduction in ZD could hinder photosynthesis and reduce the contribution of photosynthetically fixed carbon from zooxanthellae to host tissue (Fitt et al., 2000; Schoepf et al., 2015). When density and photosynthetic intensity of coral symbiotic zooxanthellae are reduced, corals are forced to enhance heterotrophic predation and then obtain more external carbon to compensate for the reduction in phototrophic carbon (Hughes et al., 2003; Hughes and Grottole, 2013). *Favia palauensis* corals could increase heterotrophic predation to maintain their normal energy budget, which is an effective compensation for the reduced photosynthesis of corals with low ZD values in the Xisha and Nansha coral reefs.

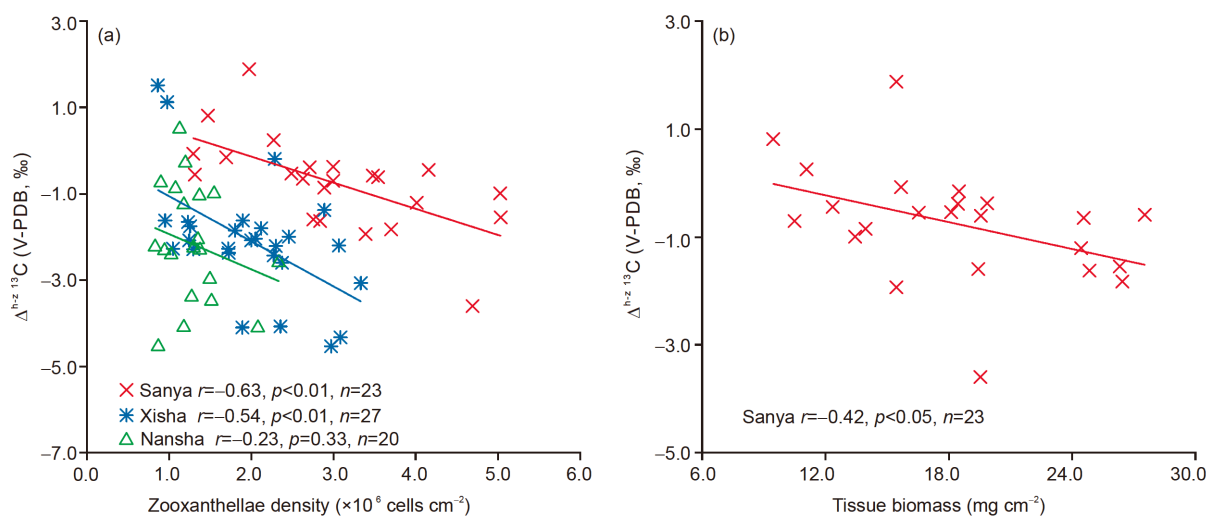
Heterotrophy is a good supplement for maintaining metabolic energy and optimizing coral adaptability (Grottole et al., 2004, 2006; Houlbrèque and Ferrier-Pagès, 2009; Nahon et al., 2013). Many studies have shown that heterotrophic competence is proposed as a mechanism that can assist corals in enhancing their resistance to environmental pressure, as well as helping coral survival and recovery after thermal bleaching (Hoegh-Guldberg, 1999; Palardy et al., 2008;

Seemann, 2013; Krueger et al., 2018). In our study, relatively high heterotrophic ability of corals is indicated by relatively low  $\delta^{13}\text{C}_h$  and  $\Delta^{h-z}^{13}\text{C}$  values in the Xisha and Nansha Islands, implying that corals can adjust their trophic status to improve their adaptability to environmental pressure. However, it should be emphasized that more research on different kinds of corals, such as relatively stress-tolerant massive corals and relatively vulnerable plating and branching corals, is needed to verify the inferences made in this paper.

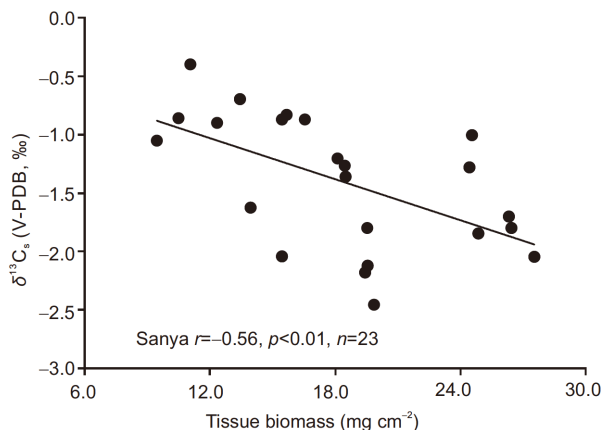
#### 4.4 Relationship between organic matter production by coral symbionts and the trophic status of corals

To better understand the relationship between organic matter production by coral symbionts and the trophic status of corals, we analyzed the correlations between ZD and  $\Delta^{h-z}^{13}\text{C}$  of each coral sample, as well as the correlation between tissue biomass and  $\Delta^{h-z}^{13}\text{C}$  (samples from Sanya,  $n=23$ ). Results show that  $\Delta^{h-z}^{13}\text{C}$  is negatively correlated with both ZD and tissue biomass, as shown in Figure 5. The negative correlation between  $\Delta^{h-z}^{13}\text{C}$  and tissue biomass (as well as ZD) indicates that corals with high tissue biomass (as well as ZD) ingest large amounts of external food with relatively low  $\delta^{13}\text{C}$  values. In fact, many studies have shown that tissue biomass is positively related to heterotrophic predation intensity (e.g., Houlbrèque and Ferrier-Pagès, 2009; Schoepf et al., 2013). Therefore, we conclude that the amount of organic material produced by coral symbionts could affect coral trophic status to some extent.

In addition, the relationship between the amount of material generated by corals and their trophic status was further confirmed. We analyzed the correlation between coral tissue biomass and  $\delta^{13}\text{C}_s$  of samples from Sanya. The results showed that coral tissue biomass was negatively related to  $\delta^{13}\text{C}_s$  values, as shown in Figure 6. Dissolved inorganic



**Figure 5** (a) Correlations between zooxanthellae density and  $\Delta^{h-z}^{13}\text{C}$  values of each coral sample from three coral reefs; (b) correlations between tissue biomass and  $\Delta^{h-z}^{13}\text{C}$  values of samples from Sanya.



**Figure 6** Correlations between tissue biomass and skeletal  $\delta^{13}\text{C}_s$  values of coral samples from Sanya.

carbon (DIC) for coral calcification comes from two different sources: external seawater DIC and internal respired  $\text{CO}_2$  (Gattuso et al., 1999). The addition of coral tissue biomass not only increases the supply of external DIC by increasing the number of transport molecules but also increases the supply of internal DIC by increasing the coral respiration rate (Furla et al., 2000; Houlbrèque and Ferrier-Pagès, 2009; Sawall et al., 2011). Generally, the higher the tissue biomass is, the higher the calcification rate (Levas et al., 2013). The kinetic isotope effect is an important factor that can influence  $\delta^{13}\text{C}_s$  values, which is related to the coral skeleton calcification rate (Schoepf et al., 2014). Kinetic fractionation is caused by the discrimination of heavy carbon isotopes during the hydroxylation and hydration of  $\text{CO}_2$  in calcification, which then leads to  $^{13}\text{C}$  depletion in the skeleton (McConnaughey, 1989a, 1989b; Linsley et al., 2019). Theoretically, strong kinetic depletion occurs in rapidly growing skeletons. That is, corals with high calcification rates have relatively low  $\delta^{13}\text{C}_s$  values (McConnaughey, 1989b; Allison et al., 1996; Cohen and Hart, 1997). In addition, corals with high tissue biomass ingest more external food with relatively low  $\delta^{13}\text{C}$  values than corals with low tissue biomass, which can also lead to relatively low  $\delta^{13}\text{C}_s$  values (Grottoli and Wellington, 1999; Reynaud-Vaganay et al., 2001). Therefore, both the kinetic effect and the ingestion of more external food can eventually lead to relatively low  $\delta^{13}\text{C}_s$  values. In this study, coral tissue biomass was negatively related to  $\delta^{13}\text{C}_s$ . These results further confirm that the more organic material produced by corals, the stronger the heterotrophic predation of the corals. According to the above results, we suggest that the organic matter produced by corals is also one of the important factors regulating the nutritional status of corals.

## 5. Conclusion

The ZD level of the Sanya fringing reefs is significantly

higher than that of the Xisha and Nansha coral reefs in the SCS. This difference is mainly attributed to the combined effects of relatively high illumination and temperature conditions in the Xisha and Nansha coral reefs, as well as relatively high nutrient levels in the Sanya fringing reefs. Relatively high values of both ZD and  $\delta^{13}\text{C}_z$  in the corals from Sanya indicate that the corals on these reefs have a stronger autotrophic photosynthetic ability than the corals in the Xisha and Nansha Islands. In contrast, relatively low  $\delta^{13}\text{C}_h$  and  $\Delta^{13}\text{C}$  values in corals from the Xisha and Nansha Islands suggest that these corals have a relatively higher heterotrophic ability than the corals in Sanya, although the concentration of available heterotrophic food sources is higher in Sanya. In addition, relatively high coral tissue biomass and low  $\delta^{13}\text{C}_s$  indicate that the more organic material produced by corals, the stronger the heterotrophic predation of the corals. Our results indicate that corals could adjust their trophic status under different environmental conditions, which is conducive to maintaining the stability of the energy supply. In addition, the trophic status of corals is related to the amount of organic material produced by coral symbionts. This trophic flexibility is essential for improving the ability of corals to adapt to different environmental conditions.

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