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Latitudinal variation in reef coral tissue thickness in the South China Sea: Potential linkage with coral tolerance to environmental stress

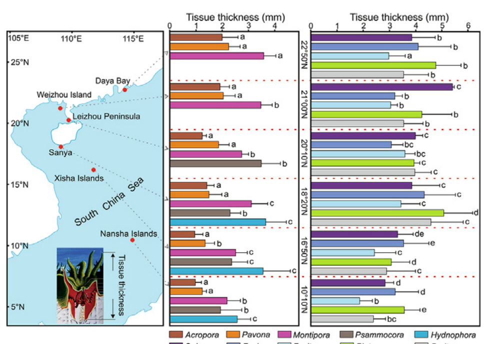
Zhenjun Qin[a,b,c], Kefu Yu[a,b,c,*], Yanting Liang[a,b,c], Biao Chen[a,b,c], Xueyong Huang[a,b,c]

[a] Coral Reef Research Center of China, Guangxi University, Nanning 530004, China
[b] Guangxi Laboratory on the Study of Coral Reefs in the South China Sea, Nanning 530004, China
[c] School of Marine Sciences, Guangxi University, Nanning 530004, China

HIGHLIGHTS

- There are significant geographic and intergeneric differences in CTT in the SCS.
- The CTT in the SCS is shaped by local environment conditions.
- Corals in the northern SCS have mainly suffered from destructive human activity.
- Corals in the southern SCS are mainly threatened by thermal stress.
- Variation in CTT in the SCS affects the stability of coral communities under stress.

GRAPHICAL ABSTRACT



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ABSTRACT

Coral tissue thickness (CTT) is an effective indicator of the adaptability of corals to environmental stress, but the relationships between the spatial and intergeneric variation of coral tissue across latitudes and tolerance to environmental stress are not well understood. To investigate this, the CTT of 768 specimens of 10 typical coral genera and surrounding seawater parameters were measured in six coral reef regions (CRRs) across the 9–22°N latitudes in the South China Sea (SCS). Results showed significant differences in CTT between different genera of corals and CRRs. CTTs were significantly higher in the northern SCS than in the southern SCS. There was also notable intergeneric variation, with the abundance of branching *Acropora* and foliaceous *Pavona* being significantly lower than that of massive *Porites*, *Galaxea*, *Favia*, *Favites*, *Hydnophora*, *Platygyra*, and encrusting *Montipora*, *Psammocora* across these CRRs. Redundancy analysis showed that dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), sea surface temperature (SST), turbidity, and transparency were the main factors affecting CTT. Overall CTT, irrespective of genus, was significantly positively correlated with DIN, SRP, and latitude, but was significantly negatively correlated with transparency and SST. Further analysis suggested that corals in the southern SCS are mainly threatened by thermal stress, whereas in the northern SCS, corals have often suffered from destructive anthropogenic disturbance. Although seawater conditions were normal during on-site investigation, a large number of branching corals (e.g., *Acropora* corals) have been lost in the last several decades due to destructive human activity. In contrast, massive and encrusting corals may have higher energy reserves and photo-protective capacities due to their thicker tissues, and consequently have higher tolerance to environmental stress. Therefore, the coral communities of the SCS have gradually been transformed from branching corals to massive/encrusting corals.

* Corresponding author at: School of Marine Sciences, Guangxi University, Nanning 530004, China.
E-mail address: kefuyu@scsio.ac.cn (K. Yu).

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1. Introduction

Coral reefs are the most diverse and productive environments in the world and are an important component of the global ecosystem (Berkelmans and Oliver, 1999; Hoegh-Guldberg, 1999). However, many coral reefs are either threatened by or have already been rapidly degraded by global warming and anthropogenic disturbance over the past 50 years (Brown, 1997a; Bellwood et al., 2004; Hoegh-Guldberg et al., 2007). Abnormally high water temperatures caused by global warming are the main cause of coral reef degradation. When suffering from high temperature stress, corals experience mass discharge of Symbiodiniaceae (i.e., zooxanthellae) and consume large amounts of energy, resulting in coral bleaching or death (Brown, 1997a; Douglas, 2003). In addition, destructive anthropogenic disturbances are also an important cause of coral reef degradation (Hoegh-Guldberg et al., 2007; Bell et al., 2014). In coastal coral reef regions (CRRs), heavy metals, persistent organic pollutants, antibiotics, sediments, and nutrients loaded into reef waters are known to be harmful to corals (Weber et al., 2012; Wiedenmann et al., 2013). Furthermore, large amounts of suspended solids (SS) reduce the sunlight available to coral-associated holobionts for photosynthesis (Nystrom et al., 2000; Fabricius et al., 2014). In response to these thermal and anthropogenic stressors, coral tissue thickness (CTT) is regulated by coral polyps (Loya et al., 2001; Rotmann and Thomas, 2012; Rotmann, 2004; Fabricius, 2005). Variations in CTT reflect the ability of corals to adapt to local environments, and consequently are closely related to the tolerance of corals to environmental stress.

Changes in latitude may result in variations in some important environmental conditions of CRRs, such as solar radiation, temperature, and aragonite saturation (Muir et al., 2015). Coral tissue is shaped by local conditions, and coral tissue, in turn, affects the ability of corals to respond to thermal and other environmental stress (Rotmann and Thomas, 2012; Barshis et al., 2013; Sawall et al., 2014). Moreover, the CTT may vary according to local environmental conditions, which may also affect the health of coral reefs. Previous studies have mainly focused on a single specific coral reef area to investigate the relationship between the CTT and local environmental stress (e.g., Loya et al., 2001; Rotmann and Thomas, 2012). Despite these studies, the relationships between spatial variations in CTT and environmental conditions remain unclear. It is not yet known which environmental factor is responsible for the observed differences in CTT. Insights into the adaptability of corals to different conditions can be gained through a better understanding of the relationship between CTT and resistance to environmental stress.

Previous studies have shown that thermal stress tolerance in corals varies between survival conditions as for congeneric corals, but also in coral taxa in a same CRR (Hughes and Connell, 1999; Loya et al., 2001; Hughes et al., 2003). Coral thermal tolerance and adaptability to local environments can be assessed by the physiological characteristics of the coral (West and Salm, 2003). However, it can be a challenge to verify changes in tolerance to thermal and environmental stress in congeneric corals in different CRRs *in-situ* due to difficulties associated with sampling. Previous studies have suggested that factors such as coral tissues, Symbiodiniaceae density and clade, coral-associated bacteria can be used as physiological indicators to assess thermal tolerance (Loya et al., 2001; Stimson et al., 2002; Berkelmans and Oppen, 2006; Liang et al., 2017). Of these, CTT has been found to be an important stress-response indicator of coral bleaching (Loya et al., 2001), high SS and sediment (Barnes and Lough, 1999), reflection by shadowing (True, 2004), and competition with turf algae (Quan-Young and Espinoza-Avalos, 2006). Therefore, the CTT, which can be measured *in situ*, is a fast and effective physiological indicator of coral reef health and tolerance to environmental stresses caused by global warming and human disturbances.

Coral reefs in the South China Sea (SCS, ~3°N–24°N) are mainly distributed in nine areas, including the Nansha Islands (i.e., Spratly Islands), Xisha Islands (i.e., Paracel Islands), Zhongsha Islands, Dongsha Islands, Hainan Island, Taiwan Island, Coast of South China, Vietnam and the Philippines, covering an area of about 8000 km^2. In the past few decades, macroecological monitoring data have shown that the coral reefs in the SCS are in severe decline (Yu, 2012). The northern SCS has experienced long-term coral degradation of live coral cover (LCC), which has declined 60%–80% (Chen et al., 2009; Yu, 2012; Zhao et al., 2012). Coral communities have changed from complex structures dominated by multiple coral taxa to single structures dominated by massive corals. In contrast, the southern SCS exhibits a high degree of coral diversity that includes branching, foliaceous, encrusting, and massive corals. However, reef corals are subject to bleaching resulting from thermal stress, especially when sea surface temperature (SST) increases dramatically over a short period of time (Yu et al., 2006; Li et al., 2011). This suggests that corals may be affected by anthropogenic or thermal stress regardless of their location in the SCS.

In the current study, two fundamental questions are addressed: (i) the effects of geographic and intergeneric variation on CTT and the local environmental factors affecting CTT variation in the SCS; and (ii) the relationships between CTT, CRRs, and tolerance to environmental stress in the SCS among coral species. We tested the hypotheses that: (i) variation in local environmental factors influence the CTT across the SCS; and (ii) the variations in the CTT of different coral genera/morphologies might affect tolerance to environmental stress. In order to explore these questions, the CTT of 10 coral genera, local environmental parameters, and information about the dominant coral genera were analyzed from six CRRs in the SCS. Our results indicate the variation in tolerance to the stress of global warming and local anthropogenic disturbances among coral genera/morphologies, and contribute to a better understanding of the cause of transformation in coral community structures in different CRRs.

2. Materials and methods

2.1. Study sites

Six CRRs containing coastal and offshore reefs in the SCS were selected for investigation (Fig. 1, Table S1). The CRRs in the northern SCS were Daya Bay, Weizhou Island, Leizhou Peninsula, and Sanya. Daya Bay (22°31′N–22°50′N, 114°30′E–114°50′E) is a semi-enclosed bay with sparsely distributed coral reefs with simple community structures, besides a narrow growth zone (Chen et al., 2009). Coral communities not associated with the reef are distributed in patches along the offshore islands and in some coastal areas due to highly variable annual SST (ranging from 13 °C in winter to 31 °C in summer). LCC decreased from 77% to 15% between 1983/1984 and 2008 (Chen et al., 2009). Four distinct

Table 1
Two-way analysis of variance (ANOVA) of the effect of sampling regions on coral tissue thickness (CTT) in Daya Bay, Weizhou Island, Leizhou Peninsula, Sanya, Xisha Islands, and Nansha Islands.

	Sum of Squares	*df*	Mean Square	F	p
Region (R)	124.76	(5, 763)	24.95	48.14	<0.001
Genus (G)	314.26	(9, 759)	34.92	67.36	<0.001
R × G	71.76	(40, 728)	1.79	3.46	<0.001

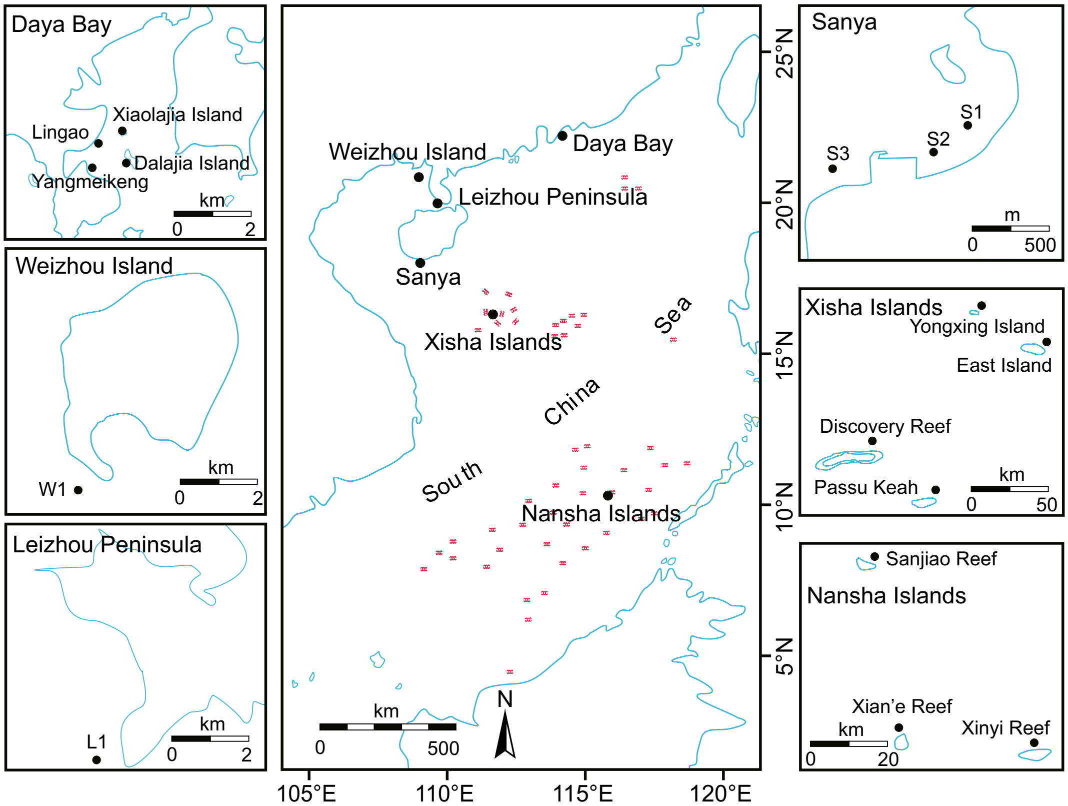

Fig. 1. Location of reefs and sampling sites in the South China Sea (SCS).

islands and reefs in Daya Bay were included, Dalajia Island (DLJ), Xiaolajia Island (XLJ), Yangmeikeng (YMK), and Ling'ao (LA). Weizhou Island (20°54′N–21°10′N, 109°00′E–109°15′E) is a volcano located in the Beibu Gulf, with an area of 26 km^2. The annual mean SST is 24.5 °C, ranging seasonally from 15 °C in winter to 30 °C in summer. Coral reefs are distributed around this island but the LCC has decreased rapidly from 60%–80% to 8%–18% over the past two decades (Wang et al., 2016). Leizhou Peninsula (20°10′N–20°27′N, 109°50′E–109°56′E) contains coral reefs situated primarily on the west coast of the peninsula and are distributed evenly from north to south; this region has been protected as part of the National Coral Reef Natural Reserves (NCRNR) since 2007. Mean annual SST is about 26 °C, ranging from the lowest 18 °C in January to the highest 30.5 °C in July (Zhao et al., 2006). Sanya (18°12′N, 109°28′E–109°30′E) is a fringing reef in Luhuitou with corals distributed around a depth of 6 m (Zhao et al., 2014; Yan et al., 2016). Coral reefs in this region have also declined seriously as a result of increasing destructive anthropogenic disturbance from the 1960s and this reef has been protected as part of the NCRNR since 1990 (Zhao et al., 2012). Mean annual SST is relatively high at 27 °C, and the monthly SST ranges from 23.1 °C (January) to 29.8 °C (August) (Yu et al., 2010).

The Xisha and Nansha Islands were included as offshore CRRs. The Xisha Islands (15°40′N–17°10′N, 110°E–113°E) are located in the northwestern part of the SCS, approximately 300–400 km from Hainan Island. Four islands and reefs in the Xisha Islands were included: Yongxing Island (YX), East Island (EI), Discovery Reef (DR), and Passu Keah (PK). Mean annual SST is 27.5 °C, with the lowest temperature of 24.7 °C and the highest temperature of 29.8 °C, which are suitable for corals growing and developing (Yu, 2012). The Nansha Islands, located in the southern SCS 1000–1600 km from Hainan Island, were the most remote survey area included in this study. This CRR includes Sanjiao Reef (SJ, 10°11′N, 115°16′E), Xian'e Reef (XE, 9°22′N, 115°26′E), and Xinyi Reef (XY, 9°20′N, 115°55′E). The Nansha CRRs are well developed, oligotrophic tropical marine reefs in which nutrients are generally scarce. Nansha reef corals exhibit high species biodiversity that is distributed from the surface to below 20 m depth. Local annual mean SST is 28.6 °C and ranges from 26.9 °C to 29.8 °C (Li et al., 2011).

2.2. Local environmental data collection

SSTs were obtained using satellite-derived data sets from NASA (https://giovanni.gsfc.nasa.gov), ocean color radiometry, and monthly averaged MODIS-Aqua at 9 km spatial resolution. The study period was from May to August 2015. General environmental parameters were measured during *in situ* investigation (Table S2), including water temperature, depth, salinity, dissolved oxygen (DO), pH, transparency, turbidity, dissolved inorganic nitrogen (DIN), and soluble reactive phosphorus (SRP). Water temperature, depth, and salinity were measured by Conductivity-Temperature-Depth/Pressure (CTD), whilst DO was assessed with a portable DO200A (YSI Inc., Yellow Springs, OH, USA). The pH was measured with separate portable meters (PHB-4). Turbidity was measured by a portable turbidity meter (WGZ-20B, 0–20 NTU). Transparency was measured with a Secchi disc (SD 30). DIN and SRP were measured with a continuous flow analyzer (SEAL QuAAtro; SEAL Analytical Shanghai, Shanghai, China). Data regarding environmental disturbances, mainly anthropogenic factors (e.g., sewage, tourism, eutrophication, heavy metals, organic pollutants [e.g., antibiotics], and oil pollution), were obtained from previous studies and reanalyzed (e.g., Chen et al., 2009, 2013; Wang et al., 2016; Wang et al., 2017; Yang et al., 2017; Yu, 2012; Zhao et al., 2012, 2014; Zhang et al., 2018).

2.3. Sample collection and coral tissue thickness determination

A total of 768 specimens, including 10 coral genera (*Acropora*, *Montipora*, *Pavona*, *Galaxea*, *Favia*, *Psammocora*, *Favites*, *Platygyra*, *Hydnophora*, and *Porites*, Table S3), were collected in the reef slopes of CRRs from May to August in 2015. All corals were randomly sampled at a depth of 2–6 m, and sampling points were tagged for repeated sampling. All specimen CTT data were determined by on-site measurements during sampling. CTT measurements (to the nearest 0.01 mm) were made with a vernier caliper and repeated eight times per sample (e.g., Rotmann, 2004; Rotmann and Thomas, 2012).

2.4. Coral taxonomic composition data collection

Line intercept transect surveys were conducted at 2–6 m depths in the outer flats/slopes of the CRRs according to the method described by the Australian Institute of Marine Science and recommended by the Global Coral Reef Monitoring Network (GCRMN) (English et al., 1997). Briefly, a fiberglass measuring tape (50 m) was fixed to the sea floor at study sites, and an Olympus TG-3 Zoom digital waterproof camera (Olympus Co., Tokyo, Japan) was used to record benthic videos. Live coral colonies were identified at the genus level and sub-classified morphologically as massive, foliaceous, branching, or encrusting. The taxonomic composition of coral community was calculated by the percent cover of each different genus, measured by the fraction of the length of the line that was intercepted by each genus of coral. The dominant coral genera of the coral community in the CRRs can be represented from these data. Ecological data and data indicating dominant coral genera in the Nansha Islands, Xisha Islands, Leizhou Peninsula, Sanya, Weizhou Island, and Daya Bay from the 2010s were collected during a macroecological survey in 2015 and previous data (e.g., Chen et al., 2013; Wang et al., 2016; Zhao et al., 2013, 2014; Chen et al., 2019b), and the 1980s–1990s (e.g., Chen et al., 2009; Wang et al., 2016; Yu et al., 1998; Zhao et al., 2006) were extracted and reanalyzed for comparative purposes.

2.5. Data analyses

All statistical analyses were conducted in SPSS Statistics version 19. The data used in this study included the effects of latitudes (six levels) and coral genera (ten levels) on CTT. A two-way factorial ANOVA was used to test the effect of each categorical factor on the response variables. Levene's test, Durbin-Watson's test, and Shapiro-Wilk's test were used to assess whether the data met the assumptions of homogeneity, normality, and independence, respectively. In cases where these assumptions were not met, the data were log transformed to meet homoscedasticity for the ANOVA. After validation of fundamental assumptions, the effects from the data were tested via the two-way factorial ANOVA. Scheffe and Duncan tests were used as post hoc multiple comparisons for further analysis of significance. All data are presented as mean ± standard deviation (SD) in this text. Statistical significance level was set at 0.05 ($p < 0.05$) for analyses. To test the correlations among environmental factors, sampling regions, and CTT, a redundancy analysis (RDA) or canonical correspondence analysis (CCA) was run in Canoco version 4.5.

3. Results

3.1. Distribution characteristics of coral tissue thickness and relationships with local environmental parameters

In this study, the CTT of 768 coral samples was measured from six CRRs in the SCS. Significant differences were found in the CTT from the different CRRs (Tables 1 and S4, two-way ANOVA, regions: $F = 48.14$, $p < 0.001$; genera: $F = 67.36$, $p < 0.001$; interaction: $F = 3.46$, $p < 0.001$), with CTT varying from 0.92 ± 0.31 mm to 5.21 ± 0.06 mm (Fig. 2). CTT was greatest in *Galaxea* (5.21 ± 0.06 mm) found in Weizhou Island. In the oligotrophic CRRs of the Xisha and Nansha Islands, CTT ranged from 0.92 ± 0.31 mm to 3.44 ± 1.02 mm and from 0.95 ± 0.23 mm to 3.44 ± 0.59 mm, respectively. Overall, CTT in the Xisha and Nansha Islands was clearly lower than that of congeneric corals in other CRRs in the northern SCS (Figs. 2 and 3).

Variation in CTT among 10 coral genera and six CRRs could be explained by differences in local environmental factors. A detrended correspondence analysis value of <3 suggested that the relationships between environmental factors, sampling regions, and CTT would be better analyzed by RDA than CCA. According to the RDA analysis (Fig. 4), DIN, SRP, SST, and transparency served as the main factors affecting CTT. CTT of overall coral genera had a significant positive correlation with DIN, SRP, and turbidity, but was significantly negatively correlated with transparency and SST.

Moreover, the anthropogenic disturbance data suggested that heavy metals (e.g., Cu, Pb, Zn, Cr, and As) and organic pollutants (e.g., antibiotics) were significantly higher in the surface waters of the northern SCS than in the southern SCS. Corals may be influenced by more anthropogenic disturbances in the northern SCS, i.e., relatively higher turbidity, nutrient loads, heavy metals, and organic pollutants. In summary, changes in environmental factors caused by natural and anthropogenic disturbances which affect water quality in the northern and southern SCS influenced the CTT.

3.2. Coral tissue thickness in the northern SCS

The CRRs in the northern SCS included in this study (Daya Bay, Weizhou Island, Leizhou Peninsula, and Sanya) were all coastal reefs near the mainland. The CTT in these reef areas was significantly higher than in the Xisha and Nansha Islands (Table S5, two-way ANOVA, $p < 0.001$), and two-way ANOVA also showed significant differences in the CTT among the coastal CRRs ($p < 0.01$). The CTT of branching corals in these CRRs was, in decreasing order: Weizhou Island > Daya Bay (DLJ, XLJ, YMK, LA) > Sanya (S1, S2, S3) > Leizhou Peninsula. For foliaceous corals, the greatest CTT was found in YMK (2.44 ± 0.65 mm) and the lowest in S1 (1.23 ± 0.13 mm). The CTT of encrusting corals ranged from 2.67 ± 0.85 mm to 3.65 ± 0.53 mm. The CTT of massive corals was significantly higher than that of branching, foliaceous or encrusting corals. The mean CTT of massive corals ranged from 3.31 ± 1.03 mm to 4.34 ± 1.21 mm. These results suggest that variability in CTT may reflect different intrageneric physiology shaped by local environment factors.

3.3. Coral tissue thickness in the Xisha and Nansha Islands

Coral reefs in the Xisha Islands are far from the mainland, approximately 330 km to southeastern Hainan Island. No significant differences were found in the CTT of coral reefs at YX, EI, DR, and PK ($p > 0.05$), but there were significant differences in coral morphology at these sites (Table S5). Among the CRRs in the Xisha Islands, the greatest CTT (3.20 ± 1.03 mm) was found in massive corals at EI and the lowest CTT (0.85 ± 0.26 mm) was found in branching corals at YX. CTT at YX was not significantly different from that of EI, DR, YX, and PK ($p > 0.05$). In the Nansha Islands, coral samples were collected in reef slope in SJ, XE, and XY. In general the CTT of these three CRRs was relatively low and were not significantly different ($p > 0.05$), although massive corals at SJ had the greatest CTT (2.75 ± 0.95 mm) and branching corals at XE had the lowest CTT (0.93 ± 0.30 mm). In short, the CTT of all four

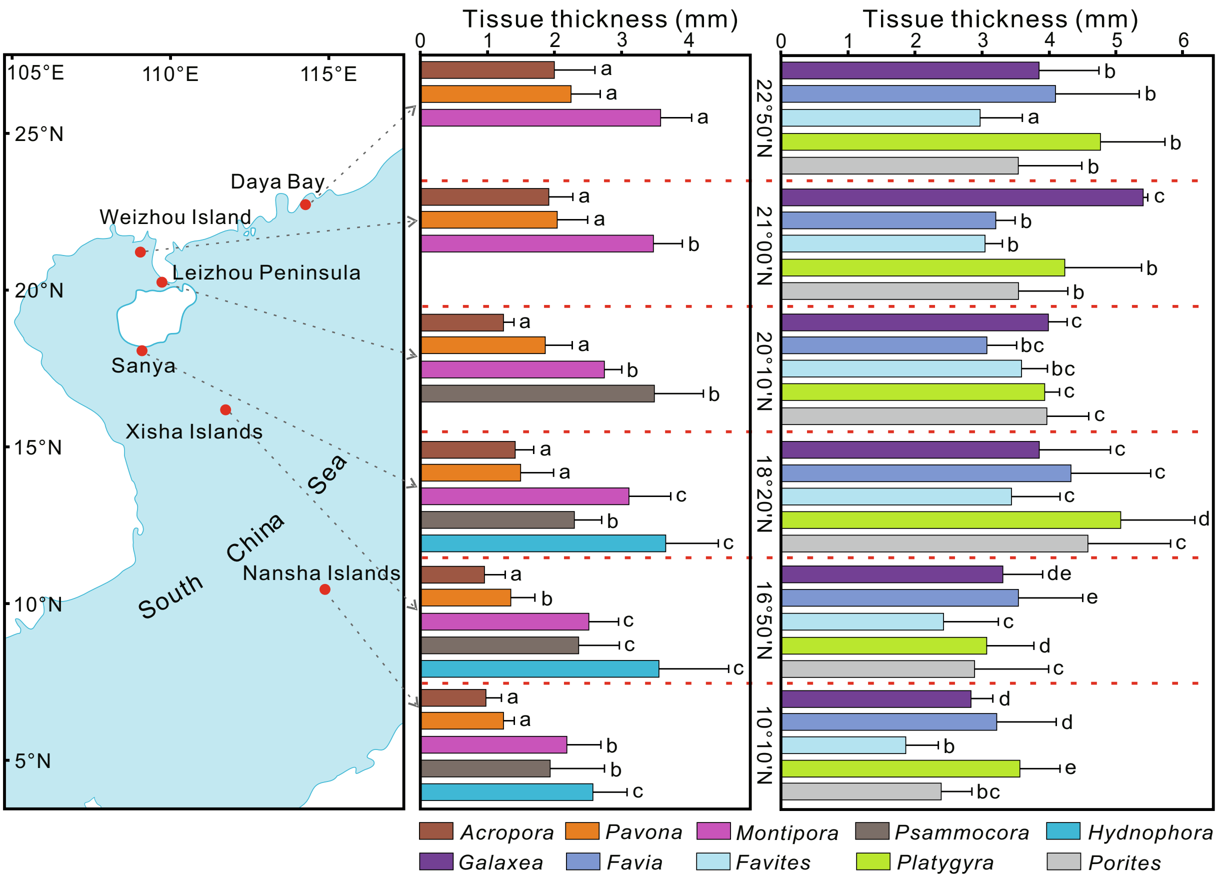

Fig. 2. Geographic distribution of coral tissue thickness (CTT) in six regions across the South China Sea (SCS). CTT is expressed as mean ± standard deviation (SD). Different letters (e.g., a, b, c) above the histograms denote statistical differences among coral genera in specific reef regions.

coral morphologies in the Xisha and Nansha Islands was significantly lower than in the northern CRRs.

3.4. Dominant coral genera in the SCS

In the northern SCS, the dominant corals had changed from branching corals to massive corals from the 1980s–1990s to the 2010s (Fig. 5). Macroecological data from the 1980s–1990s showed CRRs in the northern SCS were generally dominated by branching *Acropora* corals. By contrast, in the 2010s these same CRRs were dominated by massive corals, such as *Porites* and *Favites*, which generally have a higher tolerance to severe anthropogenic disturbances (e.g., sewage, pollutants, eutrophication, and oil pollution).

The dominant corals in the Xisha and Nansha Islands were branching corals (e.g., *Acropora*), foliaceous corals (e.g., *Pavona*), and massive corals (e.g., *Porites*, *Favia*). In the Xisha Islands, the dominant genera were *Acropora*, *Pocillopora*, *Montipora*, and *Porites*. In the Nansha Islands, the dominant genera were *Acropora*, *Montipora*, and *Porites*. Contrary to results from mainland adjacent CRRs, no major changes in the dominant coral genera in the Xisha and Nansha Islands was observed between the 1980s–1990s and the 2010s.

4. Discussion

4.1. Spatial distribution patterns of coral tissue thickness and their drivers

The 768 coral samples from the six CRRs evaluated in this study showed that significant differences in congeneric corals form geographically distinct CRRs. In general, corals in the Nansha Islands had lower CTT and corals in the northern SCS had higher CTT. However, different species of corals in the northern CRRs had the highest CTT, (e.g., *Platygyra* and *Galaxea* had the highest CTT in Sanya and Weizhou Island, respectively).

Several factors influence the geographic variation in CTT we observed. RDA analyses indicated that the main causes of low CTT in the Nansha and Xisha Islands were high SSTs and transparency. In the Nansha Islands, summer SSTs exceed 31 °C at times, a temperature high enough to cause bleaching (Li et al., 2011). Under this thermal stress, the CTT in the Nansha Islands has become thinner than that of other coral reefs. Specifically, *Acropora*, *Montipora*, *Galaxea*, and *Porites* in the Nansha Islands had CTT that was 30%–50% lower than that of corals in the northern SCS (e.g., Weishou Island and Daya Bay). In higher temperatures, many coral physiological functions decline and the growth rates of corals are reduced (Coles and Brown, 2003; Rodrigues and Grottoli, 2007; Wooldridge, 2014; Yan et al., 2019). Furthermore, corals under thermal stress will consume energy reserves, which reduces CTT (Rodrigues and Grottoli, 2007). Additionally, high transparency results in excessive solar radiation that can cause a 15%–25% reduction in CTT and affect normal survival of corals (Darke and Barnes, 1993; Coles and Brown, 2003).

While it is known that CTT is related to local water conditions, no significant negative impact on corals in the northern SCS was observed during on-site investigation, and the CTT of CRRs in the SCS were within normal range. Previous studies have shown that water quality parameters, particularly suspended solids, turbidity, nutrients, and pollutants, significantly influence CTT (Barnes and Lough, 1992; Anthony, 2000; Rotmann and Thomas, 2012). In gen-

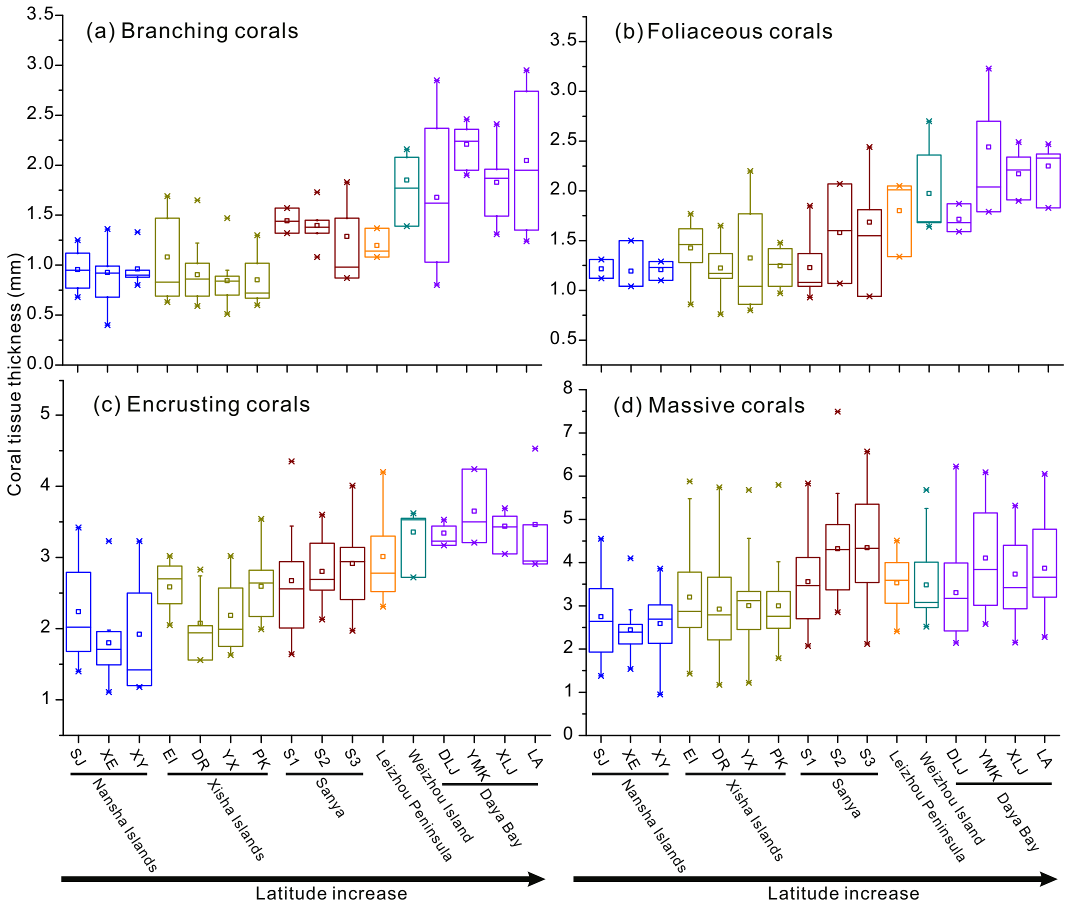

Fig. 3. Distribution of coral tissue thickness (CTT) among different coral morphologies in the South China Sea (SCS). The reef regions included in this study were: Nansha Islands – Sanjiao Reef (SJ), Xiane Reef (XE), Xinyi Reef (XY); Xisha Islands – Yongxing Island (YX), East Island (EI), Discovery Reef (DR), and Passu Keah (PK); Daya Bay – Dalajia Island (DLJ), Xiaolajia Island (XLJ), Yangmeikeng (YMK), and Ling'ao (LA); Weizhou Island; Leizhou Peninsula; Sanya (S1, S2, S3).

eral, high concentrations of pollutants or contaminants from accidents have obvious negative effects on corals. For example, Rotmann and Thomas (2012) found that CTT was significantly reduced in waters with high concentrations of mine-related turbidity stress (>25 mg L^{-1}) at Lihir Island, Papua New Guinea. By contrast, there is some evidence that modest turbidity can be conducive to coral predation and positively influence corals in good water conditions. Fabricius (2005) implied that modestly elevated particulate organic matter (POM) does not causes coral tissue damage or death, rather that it may provide organic matter as a food source. In our study, although water quality parameters showed that turbidity, DIN, and SRP were significantly higher and that transparency was significantly lower in the southern SCS than at Sanya, Leizhou Peninsula, Weizhou Island, and Daya Bay, the environmetal stress caused by anthropogenic disturbances may have been below the threshold of severe harm to corals, not affecting CTT in the CRRs during the research period. Moreover, the relatively high POM and nutrients on the coastal reefs could contribute to coral tissue increase. In support of this, it was noted that corals in the northern SCS were generally thicker than congeneric corals in the Xisha and Nansha Islands.

4.2. Inter-genera/morphological variation of CTT and distinct tolerances to thermal stress

Over the long-term, corals have adapted to changing environments by evolving into different morphological types with various polyps. The morphological variation of coral polyps affects coral morphology and tissue thickness and is consequently linked to tolerance to thermal stress (Berkelmans and Oliver, 1999; Gates and Edmunds, 1999; Loya et al., 2001). We observed significant differences in CTT between the coral genera on the six reefs sampled in this study. At the Xisha Islands, the lowest CTT was recorded in *Acropora*, and the highest in *Favi*a, which had a CTT approximately three times higher than *Acropor*a. In Daya Bay, *Platygyra* had the highest CTT and again the lowest was in *Acropora*, approximately two times lower than the CTT of *Platygyra*. The CTT of other coral genera in Daya Bay was, in increasing order, *Montipora*, *Pavona*, *Galaxea*, *Favites*, and *Porites*. In general, the CTT in each CRR followed the pattern of branching corals < foliaceous corals < encrusting corals < massive corals. CTT affects the ability of corals thermal stress tolerance. Loya et al. (2001) found that the thicker massive corals (i.e., *Favites chinensis*, *Platygyra ryukyuensis*, and *Goniastrea aspera*) survived after exposure to the air and high amounts of radiation during summer afternoon low tide in an intertidal zone in Sesoko, showing high tolerance of these genera to environmental stress. In our study, the massive *Galaxea*, *Favia*, *Platygyra*, and *Porites* corals with thicker tissues could potentially be more tolerant to thermal stress than the foliaceous and encrusting corals, while branching corals, such as *Acropora* with thin tissues, would be the most susceptible to thermal stress.

There are two possible mechanisms that may explain variations in tolerance to thermal stress. On the one hand, CTT is closely related to the energy reserve of corals, and thermal stress responses partly depend on the available energy reserves (Rotmann and Thomas, 2012). Greater CTT, therefore, implies

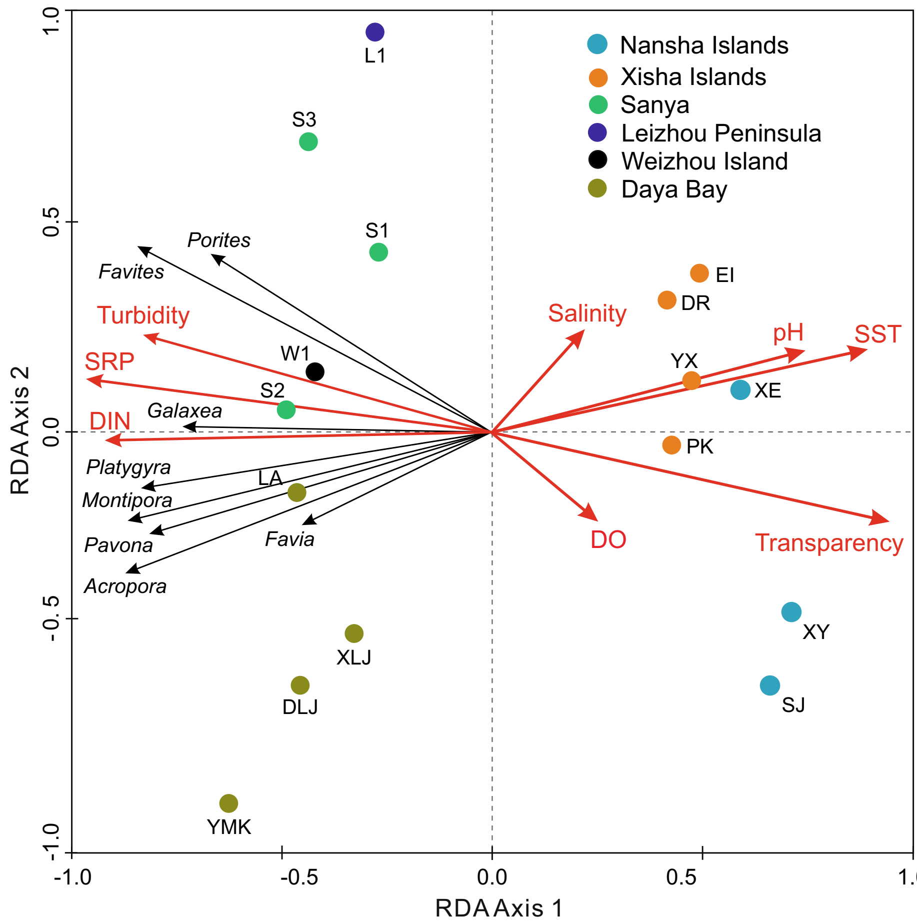

Fig. 4. Correlations among environmental parameters, coral tissue thickness (CTT), and sampling regions. Redundancy analysis (RDA) was performed to identify correlations among environmental parameters, CTT, and coral genera at different coral reef regions (CRRs). The first axis (RDA Axis 1) explains 59.1% of the total variation, the second axis (RDA Axis 2) explains 9.4% of the total variation.

higher energy reserves and higher thermal tolerance in thick-tissue corals (Oliver et al., 1983; Loya et al., 2001). On the other hand, different coral species exhibit different photo-protective capabilities, with thicker tissue corals generally being more protected against radiation (Hoegh-Guldberg, 1999; Dimond et al., 2012). We found that corals with higher CTT had denser Symbiodiniaceae populations (Qin et al., 2019), which may confer a higher tolerance to severe solar radiation stress in the southern SCS. Some massive corals (e.g., *Porites*, see Gong et al., 2018; Chen et al., 2019a) with thicker tissues are also stably associated with heat-resistant Symbiodiniaceae, which can increase tolerance to thermal stress. The expansion and contraction of coral tissue provides a fast and flexible means to regulate the radiant flux reaching the Symbiodiniaceae. When coral tissues are in a contracted state, the Symbiodiniaceae create a self-shadow for radiation protection. Thick tissue corals can contract more effectively than thin corals, and hence can achieve better self-shadowing. This effect could protect the symbiotic Symbiodiniaceae from solar radiation. Additionally, thick tissue corals will maintain photosynthesis for longer than thin tissue corals, which removes some toxic oxygen free radicals from the system and may offer increased photo-protective effects (Shick et al., 2010).

4.3. CTT variation affects coral health state and community structure under global warming and destructive anthropogenic disturbance

Interspecific and geographic variation of CTT in the SCS may affect coral health. Our study results showed that CTT in the northern SCS was significantly higher than in the southern SCS. According to the analysis of tissue thickness as an indicator of coral health, corals in the northern SCS were in a healthier state than those in the southern SCS. Corals in the Xisha and Nansha Islands were subjected to thermal stress and were in sub-health state. Due to differences in tolerance to thermal stress between coral morphologies, massive corals with low growth rates and high metabolic rates are more adaptable to environmental stress than faster growing branching corals with low metabolic rates (Gates and Edmunds, 1999; Loya et al., 2001). When threatened by thermal stress, reduced CTT makes branching corals (e.g., *Acropora*) more susceptible to death. Mass loss of branching corals in areas that suffer frequently from abnormally high thermal stress may result in coral reef rapid degradation. The tropical CRRs in the Great Barrier Reef, for instance, were seriously affected by thermal bleaching events in 1998, 2010, and 2015–2016 (Hughes et al., 2017). In 2016 alone, a thermal event caused bleaching or death of ~51%–60% of corals, especially the foliaceous and branching corals, and the coral community structure shifted. Such global thermal bleaching events have also affected coral survival in the southern SCS, especially that of heat-sensitive *Acropora*. For example, Li et al. (2011) found that the branching *Acropora* and *Pocillopora* had higher bleaching ratios (21% and 23%, respectively) than did the massive *Favia* and *Porites* (the ratios < 10%) during a 2010 bleaching event in the Nansha Islands. In 2015, DeCarlo et al. (2017) reported that abnormally high temperatures (~2 °C higher than normal) in the Dongsha Atoll of the SCS caused ~40% of corals to be bleached. Their study also showed that the most seriously

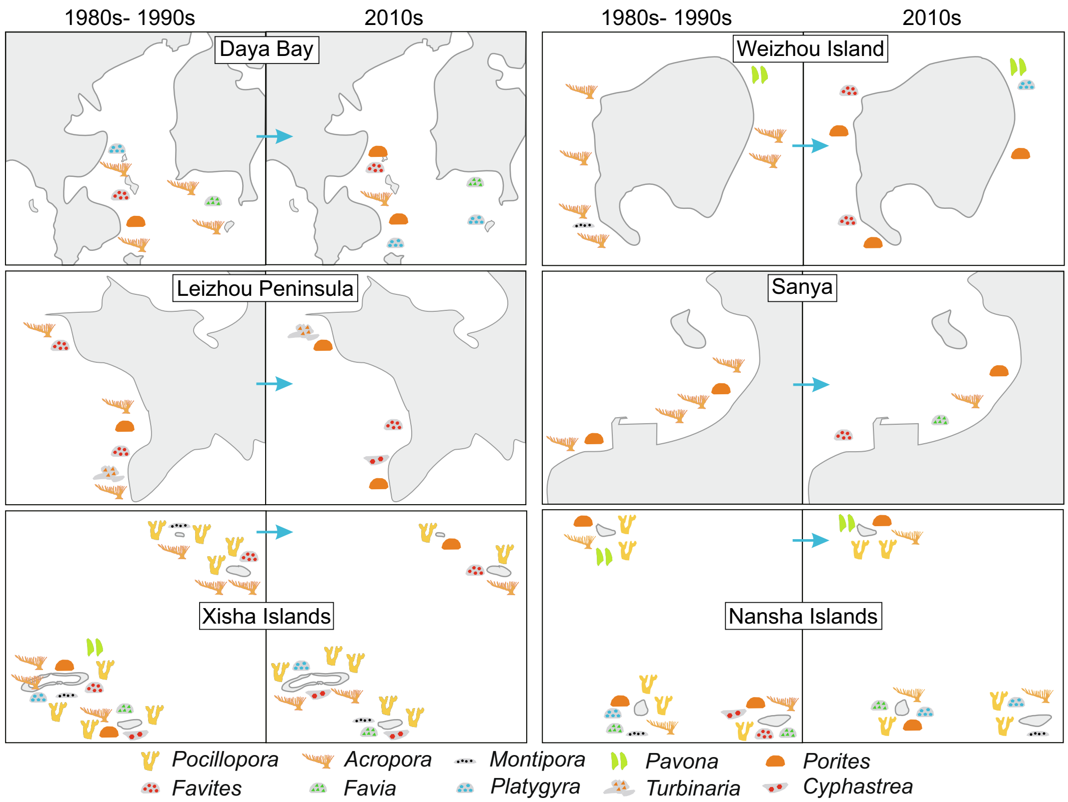

Fig. 5. Schematic diagram of the changes in dominant coral genera in the six studied coral reef regions (CRRs) from the 1980s–1990s to the 2010s.

affected coral genera were *Pavona* (~95%) and *Acropora* (~61%), and the least affected were *Porites* (~20%). Corroborating these findings, our results suggest that the corals that are most susceptible to bleaching are with those with lower CTT. In contrast, corals in the northern SCS have thicker CTT and are more resistant to thermal and other environmental stresses, and are, hence, in a relatively healthy state.

However, sudden and devastating anthropogenic disturbances were found to cause coral community degradation and alteration in the northern SCS. In generally, healthy coral reefs are dominated by branching corals (e.g., *Acropora*), and massive corals, such as *Porites*, are less abundant. Massive corals, which have higher CTT and are more tolerant to stress, will quickly become dominant in disturbed coral reefs (Barnes and Lough, 1992; Rotmann and Thomas, 2012). Although the environmental stress caused by anthropogenic disturbances may have remained below the threshold of severe harm to corals in the northern SCS during on-site investigation, living reef corals have in fact been rapidly degrading over the past decades (Chen et al., 2009; Zhao et al., 2013). The most likely explanation for this disparity is that these reefs are adversely affected by sudden and devastating anthropogenic events, including pollution events, anthropogenic eutrophication, overfishing, or construction (Chen et al., 2009; Zhao et al., 2013; Wang et al., 2016). These destructive events can cause severe damage to branching corals with low CTT and large corals can die within a few weeks. For example, large-scale *Acropora* corals death occurred in Weizhou Island over a short period of time in 2008 due to the discharge of a large amount of crude oil into the reef (Xu et al., 2018). High concentrations of oil polluted the seawater, killing these branching corals, which have not yet recovered. In Daya Bay, the water produced by the local marine culture is harmful to branching corals and a series of previous studies have described the combined negative effects (e.g., Chen et al., 2009; Han et al., 2017; Ye et al., 2017). Differences in tolerance to pollution have resulted in variable survival rates among coral species. Long-term ecological surveys of Sanya, Weizhou Island, and Daya Bay, have found that severe anthropogenic disturbance results in death of large branching corals (e.g., *Acropora*) and proliferation of higher CTT corals, including *Porites*, *Galaxea*, *Platygyra*, *Favia*, and *Favites* (Chen et al., 2009; Zhao et al., 2014; Wang et al., 2016). However, though massive corals may be short-term winners in these situations (Baskin, 1998; Bellwood et al., 2010), coral reef ecosystems dominated by massive corals are not conducive for the reef community and reef development.

Conflict of Interest

The authors declare that the research was no competing financial interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.134610.

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