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

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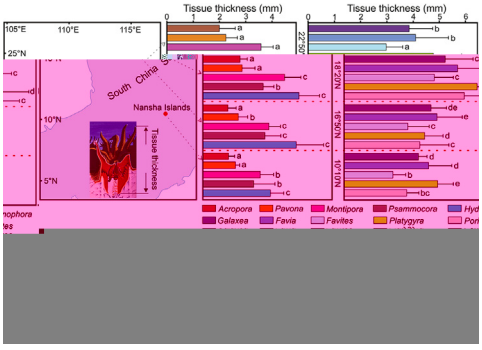
highlights

- 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 dec-

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.

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

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

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.

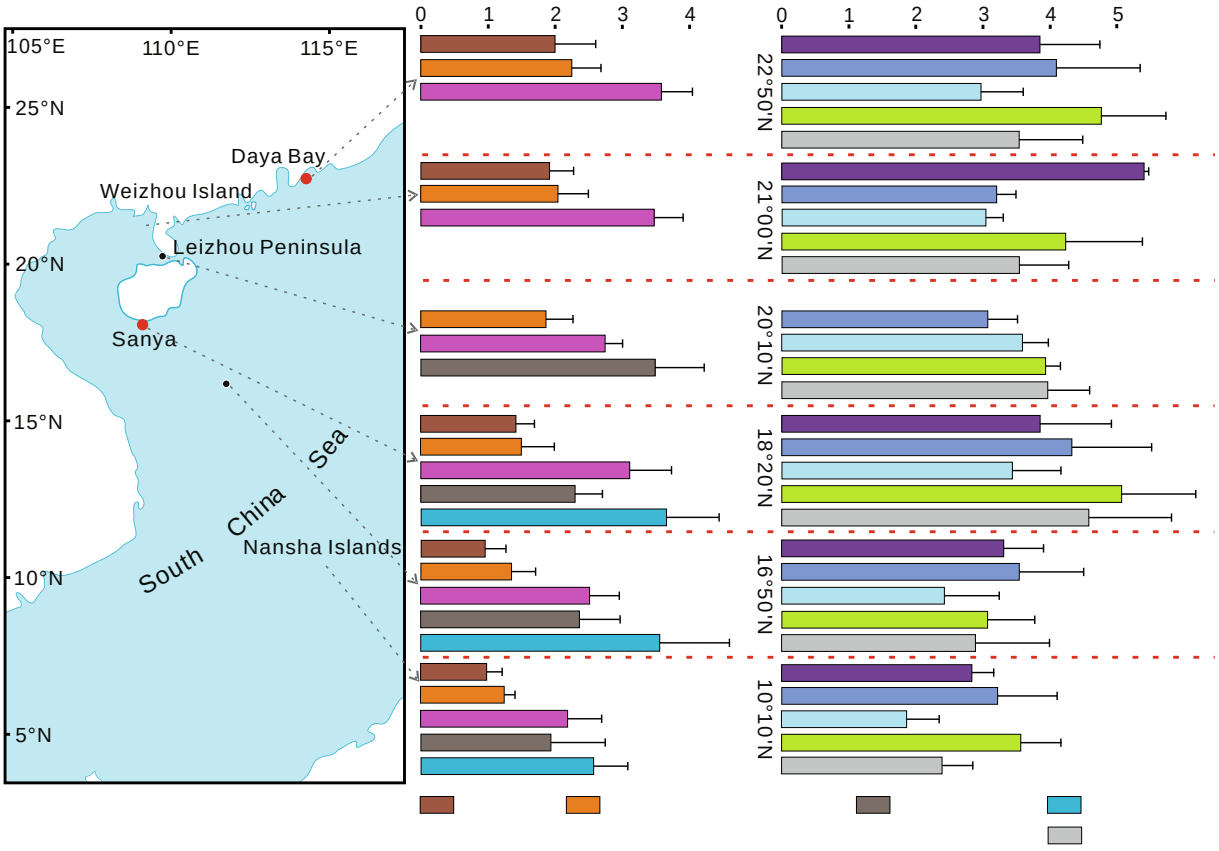
Moreover, the anthropogenic disturbance data suggested that heavy metals (e.g., Cu, Pb, Zn, Cr, and As) and organic pollutants (e.g., antibiotics) were significantly higher in the surface waters of the northern SCS than in the southern SCS. Corals may be influenced by more anthropogenic disturbances 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



coral morphologies in the Xisha and Nansha Islands was signiÞcantly 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 1980sÐ1990s to the 2010s (Fig. 5). Macroecological data from the 1980sÐ1990s 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 1980sÐ1990s 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 signiÞcant 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 inßuence 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. SpeciÞcally, Acropora, Montipora, Galaxea, and Porites in the Nansha Islands had CTT that was 30%Ð50% 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%Ð25% 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 signiÞcant 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, signiÞcantly inßuence CTT (Barnes and Lough, 1992; Anthony, 2000; Rotmann and Thomas, 2012). In gen-

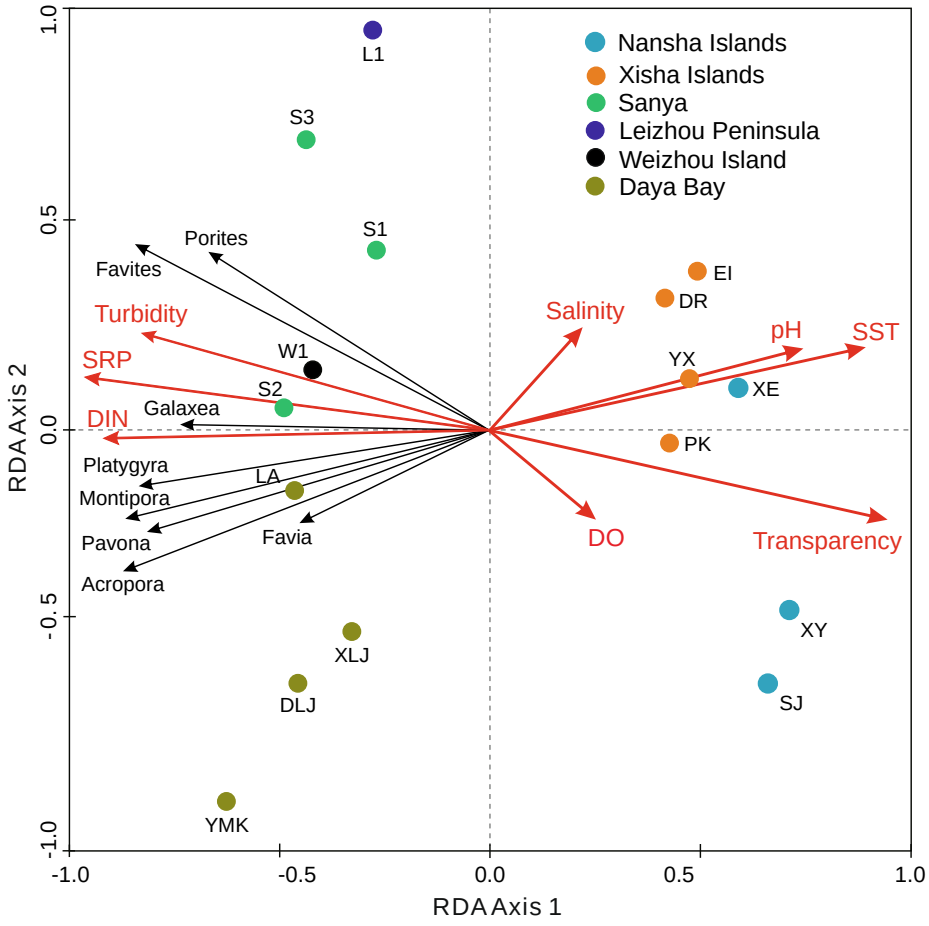
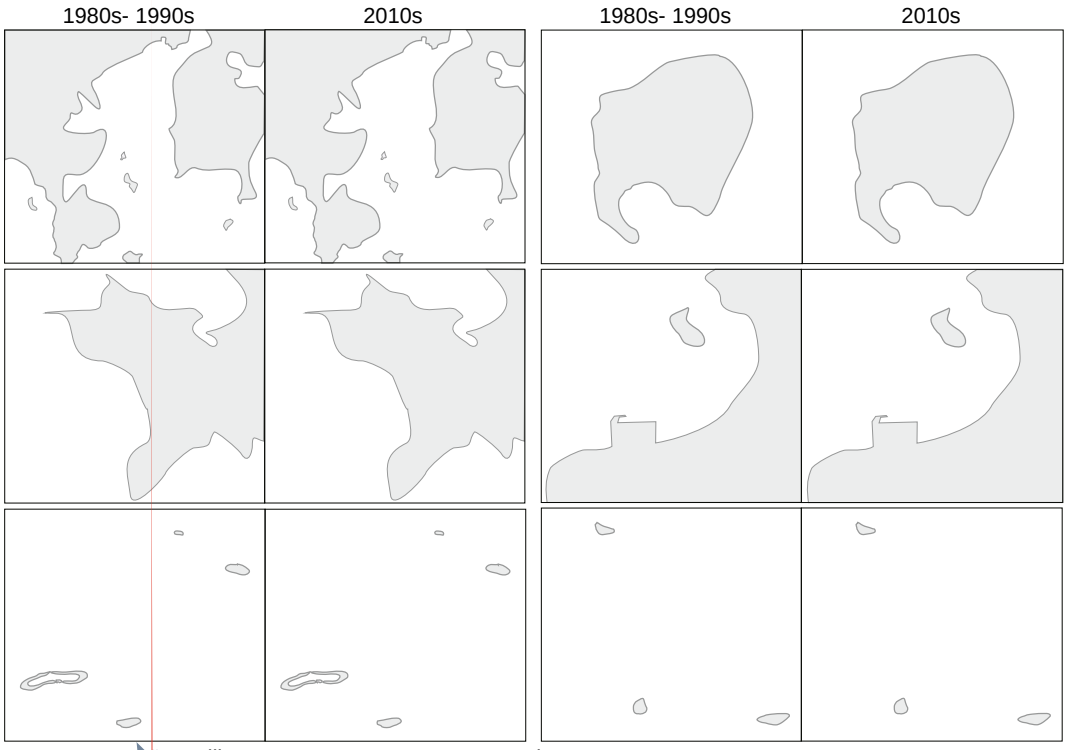


Fig. 4. Correlations among environmental parameters, coral tissue thickness (CTT), and sampling regions. Redundancy analysis (RDA) was performed to identify correlations among environmental parameters, CTT, and coral genera at different coral reef regions (CRRs). The first axis (RDA Axis 1) explains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



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 general, 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.

Acknowledgements

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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.

References

Anthony, K.R.N., 2000. Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). Coral Reefs 19, 59–67.

Barnes, D.J., Lough, J.M., 1992. Systematic variations in the depth of skeleton occupied by coral tissue in massive colonies of Porites from the Great Barrier Reef. J. Exp. Mar. Biol. Ecol. 159, 113–128.

Barshis, D.J., Ladner, J.T., Oliver, T.A., Seneca, F.O.O., Nikki, T.K., Palumbi, S.R., 2013. Genomic basis for coral resilience to climate change. P. Natl. Acad. Sci. U. S. A. 110, 1387–1392.

Baskin, Y., 1998. Winners and losers in a changing world. Bioscience 48, 788–792.

Bell, P.R.F., Elmetri, I., Lapointe, B.E., 2014. Evidence of large-scale chronic eutrophication in the Great Barrier Reef: quantification of chlorophyll a thresholds for sustaining coral reef communities. Ambio 43, 361–376.

Bellwood, D.R., Hoey, A.S., Choat, J.H., 2010. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol. Lett. 6, 281–285.

Bellwood, D.R., Hughes, T.P., Folke, C., Nystrom, M., 2004. Confronting the coral reef crisis. Nature 429, 827–833.

Berkelmans, R., Oliver, J.K., 1999. Large-scale bleaching of corals on the Great Barrier Reef. Coral Reefs 18, 55–60.

Berkelmans, R., Oppen, M.J.H.V., 2006. The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. Pro. R. Soc. B 273, 2305–2312.

Brown, B.E., 1997a. Coral bleaching: causes and consequences. Coral Reefs 16, 129–138.

Chen, T., Li, S., Yu, K., 2013. Macrobioerosion in Porites corals in subtropical northern South China Sea: a limiting factor for high-latitude reef framework development. Coral Reefs 32, 101–108.

Chen, T., Yu, K., Shi, Q., Li, S., Price, G.J., Wang, R., Zhao, M., Chen, T., Zhao, J., 2009. Twenty-five years of change in scleractinian coral communities of Daya Bay (northern South China Sea) and its response to the 2008 AD extreme cold climate event. Chinese Sci. Bull. 54, 2107–2117.

Chen, B., Yu, K., Liang, J., Huang, W., Wang, G., Su, H., et al., 2019a. Latitudinal variation in the molecular diversity and community composition of Symbiodiniaceae in coral from the South China Sea. Front. Microbiol. 10, 1278.

Chen, X., Yu, K., Huang, X., Wang, Y., Liao, Z., Zhang, R., et al., 2019b. Atmospheric nitrogen deposition increases the possibility of macroalgal dominance on remote coral reefs. J. Geophys. Res. Biogeo. 124.

Coles, S.L., Brown, B.E., 2003. Coral bleaching - capacity for acclimatization and adaptation. Adv. Mar. Biol. 46, 183–223.

Darke, W.M., Barnes, D.J., 1993. Growth trajectories of corallites and ages of polyps in massive colonies of reef-building corals of the genus Porites. Mar. Biol. 117, 321–326.

Decarlo, T.M., Cohen, A.L., Wong, G.T.F., Davis, K.A., Lohmann, P., Soong, K., 2017. Mass coral mortality under local amplification of 2 °C ocean warming. Sci. Rep. UK 7, 44586.

Dimond, J.L., Holzman, B.J., Bingham, B.L., 2012. Thicker host tissues moderate light stress in a cnidarian endosymbiont. J. Exp. Biol. 215, 2247–2254.

Douglas, A.E., 2003. Coral bleaching - how and why?. Mar. Pollut. Bull. 46, 385–392.

English, S., Wilkinson, C., Baker, V., 1997. Survey manual for tropical marine resources. Townsville, Qld: Australian Institute of Marine Science.

Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar. Pollut. Bull. 50, 125–146.

Fabricius, K.E., Logan, M., Weeks, S., Brodie, J., 2014. The effects of river run-off on water clarity across the central Great Barrier Reef. Mar. Pollut. Bull. 84, 191–200.

Gates, R.D., Edmunds, P.J., 1999. The Physiological mechanisms of acclimatization in tropical reef corals. Am. Zool. 39, 30–43.

Gong, S., Chai, G., Xiao, Y., Xu, L., Yu, K., Li, J., et al., 2018. Flexible symbiotic associations of Symbiodinium with five typical coral species in tropical and subtropical reef regions of the northern South China Sea. Front. Microbiol. 9, 2485.

Han, T., Shi, R., Qi, Z., Huang, H., Liang, Q., Liu, H., 2017. Interactive effects of oyster and seaweed on seawater dissolved inorganic carbon systems: implications for integrated multi-trophic aquaculture. Aquacult. Environ. Interact. 9, 469–478.

Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar. Freshwater Res. 50, 839–866.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., et al., 2007. Coral reefs under rapid climate change and ocean acidification. Science 318, 1737–1742.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., et al., 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301, 929–933.

Hughes, T.P., Connell, J.H., 1999. Multiple stressors on coral reefs: a long-term perspective. Limnol. Oceanogr. 44, 932–940.

Hughes, T.P., Kerry, J.T., Alvarez-Noriega, M., Alvarez-Romero, J.G., Anderson, K.D., Baird, A.H., et al., 2017. Global warming and recurrent mass bleaching of corals. Nature 543, 373–377.

Li, S., Yu, K., Chen, T., Shi, Q., Zhang, H., 2011. Assessment of coral bleaching using symbiotic zooxanthellae density and satellite remote sensing data in the Nansha Islands, South China Sea. Chinese Sci. Bull. 56, 1031–1037.

Liang, J., Yu, K., Wang, Y., Huang, X., Huang, W., Qin, Z., et al., 2017. Distinct bacterial communities associated with massive and branching scleractinian corals and potential linkages to coral susceptibility to thermal or cold stress. Front. Microbiol. 8, 979.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., Woesik, R.V., 2001. Coral bleaching: the winners and the losers. Ecol. Lett. 4, 122–131.

Muir, P.R., Wallace, C.C., Terence, D., David, A.J., 2015. Limited scope for latitudinal extension of reef corals. Science 348, 1135–1138.

Nystrom, M., Folke, C., Moberg, F., 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol. Evol. 15, 413–417.

Oliver, J.K., Chalker, B.E., Dunlap, W.C., 1983. Bathymetric adaptations of reef-building corals at davies reef, great barrier reef, Australia. I. Long-term growth responses of Acropora formosa (Dana 1846). J. Exp. Mar. Biol. Ecol. 73, 11–35.

Qin, Z., Yu, K., Wang, Y., Xu, L., Huang, X., Chen, B., et al., 2019. Spatial and intergeneric variation in physiological indicators of corals in the South China Sea: insights into their current state and their adaptability to environmental stress. J. Geophys. Res. Oceans 124.

Quan-Young, I., Espinoza-Avalos, J., 2006. Reduction of zooxanthellae density, chlorophyll a concentration, and tissue thickness of the coral Montastrea faveolata (Scleractinia) when competing with mixed turf algae. Limnol. Oceanogr. 51 (2), 1159–1166.

Rodrigues, L.J., Grottoli, A.G., 2007. Energy reserves and metabolism as indicators of coral recovery from bleaching. Limnol. Oceanogr. 52, 419–425.

Rotmann, S., 2004. Tissue thickness as a tool to monitor the stress response of massive Porites corals to turbidity impact on Lihir Island, Papua New Guinea. PhD thesis, James Cook University, Townsville, Australia.

Rotmann, S., Thomas, S., 2012. Coral tissue thickness as a bioindicator of mine-related turbidity stress on coral reefs at Lihir Island, Papua New Guinea. Oceanography 25, 52–63.

Sawall, Y., Al-Sofyani, A., Banguera-Hinestroza, E., Voolstra, C.R., 2014. Spatio-temporal analyses of Symbiodinium physiology of the coral Pocillopora verrucosa along large-scale nutrient and temperature gradients in the Red Sea. PLoS One 9, (8) e103179.

Shick, J.M., Lesser, M.P., Jokiel, P.L., 2010. Effects of ultraviolet radiation on corals and other coral reef organisms. Global Change Biol. 2, 527–545.

Stimson, J., Sakai, K., Sembali, H., 2002. Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. Coral Reefs 21, 409–421.

True, J.D., 2004. Massive Porites corals as indicators of environmental changes. PhD Thesis, James Cook University, Townsville, Australia, http://eprints.jcu.edu.au/7890.

Wang, L., Yu, K., Wang, Y., Wang, S., Huang, X., Zhang, R., Wang, L., 2017. Distribution characteristic of heavy metals in coral reefs located in the Zhongsha Islands and Xisha Islands of South China Sea (in Chinese). Tropical Geography 37 (5), 718–727.

Wang, W., Yu, K., Wang, Y., 2016. A review on the research of coral reefs in the Weizhou Island, Beibu Gulf (in Chinese). Tropical Geography 36 (1), 72–79.

Weber, M., de Beer, D., Lott, C., Polerecky, L., Kohls, K., Abed, R.M.M., et al., 2012. Mechanisms of damage to corals exposed to sedimentation. P. Natl. Acad. Sci. USA 109, 1558–1567.

West, J.M., Salm, R.V., 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Conserv. Biol. 17, 956–967.

Wiedenmann, J., Dangelo, C., Smith, E.G., Hunt, A.N., Legiret, F.E., Postle, A.D., Achterberg, E.P., 2013. Nutrient enrichment can increase the susceptibility of reef corals to bleaching. Nat. Clim. Change 3, 160–164.

Wooldridge, S.A., 2014. Differential thermal bleaching susceptibilities amongst coral taxa: re-posing the role of the host. Coral Reefs 33, 15–27.

Yan, H., Yu, K., Shi, Q., Tan, Y., Liu, G., Zhao, M., et al., 2016. Seasonal variations of seawater pCO_2 and sea-air CO_2 fluxes in a fringing coral reef, northern South China Sea. J. Geophys. Res. Oceans 121, 998–1008.

Yan, H., Shi, Q., Yu, K., Tao, S., Yang, H., Liu, Y., et al., 2019. Regional coral growth responses to seawater warming in the South China Sea. Sci. Total Environ. 670, 595–605.

Yang, H., Wang, S., Yu, K., Huang, X., Zhang, R., Wang, Y., Guo, S., 2017. Pollution characteristics of heavy metals in seawater of coral growing regions in the northern South China Sea (in Chinese). Ecol. Environ. Sci. 26 (2), 253–260.

Ye, S., Zhang, L., Feng, H., 2017. Marine ecological risk assessment methods for radiation accidents. J. Environ. Rad. 180, 65–76.

Yu, K., Hua, Q., Zhao, J., Hodge, E., Fink, D., Barbetti, M., 2010. Holocene marine C-14 reservoir age variability: evidence from Th-230-dated corals in the South China Sea. Paleoceaography 25.

Yu, K., Zhao, H., Zhu, Y., 1998. Modern sedimentary characteristic of Halimeda on coral reefs of Nansha Islands (in Chinese). Acta Sedimentol. Sin. 16 (3), 20–24.

Yu, K., Zhao, J., Shi, Q., Chen, T., Wang, P., Collerson, K.D., Liu, T., 2006. U-series dating of dead Porites corals in the South China Sea: evidence for episodic coral mortality over the past two centuries. Quat. Geochronol. 1, 129–141.

Yu, K., 2012. Coral reefs in the South China Sea: their response to and records on past environmental changes. Sci. China Earth Sci. 55, 1217–1229.

Zhang, R., Zhang, R., Yu, K., Wang, Y., Huang, X., Pei, J., et al., 2018. Occurrence, sources and transport of antibiotics in the surface water of coral reef regions in the South China Sea: potential risk to coral growth. Environ. Pollut. 232, 450–457.

Zhao, H., Wang, L., Song, C., 2006. The distribution and protection of the coral reefs in the west of Xuwen County. Tropical Geography 3, 202–206.

Zhao, M., Yu, K., Zhang, Q., Shi, Q., Price, G.J., 2012. Long-term decline of a fringing coral reef in the northern South China Sea. J. Coastal Res. 28, 1088–1099.

Zhao, M.X., Yu, K.F., Shi, Q., Chen, T.R., Zhang, H.L., Chen, T.G., 2013. Coral communities of the remote atoll reefs in the Nansha Islands, southern South China Sea. Environ. Monit. Assess. 185, 7381–7392.

Zhao, M.X., Yu, K.F., Zhang, Q.M., Shi, Q., Roff, G., 2014. Age structure of massive Porites lutea corals at Luhuitou fringing reef (northern South China Sea) indicates recovery following severe anthropogenic disturbance. Coral Reefs 33, 39–44.