Chinese Science Bulletin

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Springer

Interspecies and spatial diversity in the symbiotic zooxanthellae density in corals from northern South China Sea and its relationship to coral reef bleaching

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Coral reef bleaching is usually characterized by expulsion of symbiotic zooxanthellae, loss of zooxanthellae pigmentation, or both. We collected 128 samples comprising 39 species of 21 genera of reef-building corals from Luhuitou and Xiaodonghai in Sanya of Hainan Island and Daya Bay of Guangdong Province, respectively, and analyzed the symbiotic zooxanthellae population density. The results show that: (1) the symbiotic zooxanthella density varies from 0.67×10^6 to 8.48×10^6 cell/cm^2, displaying significant interspecies variability, with branch corals usually having relatively less zooxanthellae (ranging from 0.67×10^6 to 2.47×10^6 cell/cm^2) than massive species (from 1.0×10^6 to 8.48×10^6 cell/cm^2); (2) corals inhabiting within 4 m water depth have higher levels of symbiotic zooxanthellae than those living at the bottom (~7 m depth) of the reef area; (3) there is no discernable difference in the zooxanthellae density between corals from relatively high latitude Daya Bay (~22°N) and those from relatively low latitude Sanya (~18°N) at comparable sea surface temperatures (SST); (4) in partially-bleached corals, the density of zooxanthellae shows the following order: healthy-looking part> semi-bleached part > bleached part. Based on the above results, we suggest that (1) the zooxanthellae density difference between branching and massive coral species is the main cause that branching corals are more vulnerable to bleaching than massive corals. For example, symbiotic zooxanthellae levels are low in branching *Acropora* and *Pocillopora corals* and thus these corals are more susceptible to bleaching and mortality; (2) symbiotic zooxanthellae density can also be affected by environmental conditions, such as sediment loads, diving-related turbidity, and aquaculture-related nitrate and phosphate input, and their increase may reduce symbiotic zooxanthellae density in corals.

coral reef bleaching, zooxanthellae density, interspecies diversity, spatial diversity, northern South China Sea

Coral reef bleaching, characterized by expulsion of the symbiotic zooxanthellae, loss of algal pigmentation or both[1,2], is considered as the most important ecological phenomenon over the past twenty years, and has resulted in serious coral reef degradation. By the year of 2004, there were only 30% of coral reefs in healthy status over the world [3], which has endangered the balance of marine ecosystem. Although a lot of factors, such as low sea surface temperature[4], freshwater discharge[5] and eruption of pathogens[6] can result in coral reef bleaching, and higher SST has been accepted as the most primary cause of large-scale coral reef bleaching events[7,8]. For example, the extremely high SST in the 1998 El Niño year resulted in 16% of global coral reef degrada-

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Received May 8, 2007; accepted June 11, 2007
doi: 10.1007/s11434-007-0514-4

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Supported by the Knowledge Innovation Project of the Chinese Academy of Sciences (Grant No. KZCX2-YW-318), the National Natural Science Foundation of China (Grant No. 40572102), the Ministry of Science and Technology of China (Grant No. 2006BAB19B03), and the Sino-Australia Special Collaboration Funds (Grant Nos. 4061120030 and CH050099)

tion[3] and involved almost all coral reef sites around the world[9], including Nansha Islands[10,11] and Weizhou Island[12] of the South China Sea. Further research suggests that coral reef bleaching shows significant interspecies diversity and branching corals show higher rates of bleaching and bleaching-related mortality than massive species[13−15], though the exact cause is still unclear[16]. Moreover, high SST seems not to be the sole factor causing coral reef bleaching. For example, in 1998, the average SST in the reef bleaching sites of the world ranged from 28.1 to 34.9℃[9], which shows even at the SST ideal for coral reef development, namely 28－29℃[17], and coral reef bleaching also occurred. Therefore there may be some other unknown mechanisms responsible for coral reef bleaching. Recent research in coral reef molecular biology found corals with zooxanthellae clade D have greater capacity to tolerate severe environment conditions than corals having other clades[18,19]. Thus, Baker[20] suggested that corals may adapt to high SST through changing the clades of zooxanthellae. It is also reported that symbiotic zooxanthellae density exhibits seasonal fluctuations with the lowest occurring in the summer-autumn seasons and the highest in the winter season[21,22]. In a word, the symbiotic zooxanthellae play a crucial role in coral reef bleaching and recovery. Because of this, we investigated the symbiotic zooxanthellae density in corals from Sanya to Daya Bay in the northern South China Sea, and further analyzed their interspecies and spatial diversity and their relationship to coral reef bleaching by comparing corals from different species, different ecological habitats, and different parts of the same colony. Stimson et al.[13] had reported the interspecies diversity based on limited published data, but till now no detailed investigations have been found in the literatures.

1 Location and environment

Sanya Bay (109°20′－109°30′E, and 18°11′－18°18′N), located in the southern Hainan Island (Figure 1), is typical of tropical ocean environment. Coral fringing reefs are well developed at Luhuitou and Xiaodonghai, and both reefs have been listed as the National Coral Reef Natural Reserves since 1990. Three basic biogeomorphologic units in the fringing reefs can be identified: inner reef flat, outer reef flat and reef slope[23] (Figure 2), and the deepest water depth is about 7m at the front of reef slopes. The mean annual SST is about 27.0℃, the lowest monthly SST is 22.8℃ (varying from 20.5 to 24.7℃), and the highest monthly SST is 29.8℃ (varying from 28.7 to 30.9℃). The latest survey suggests that at Luhuitou fringing reef, the living coral cover is 23.4% and the dead coral cover is 23.6% although it still preserves very high biodiversity[24]. Compared with historical records that show living coral covers around 85% between 1960 and 1970, it is clear that the fringing reef has been severely damaged. Human activities, including reef dredging, curios collecting, destructive fishing, sediment and pollutant discharge from coastal land, and recent marine aquaculture, are suggested to be the main factors responsible for the coral reef degradation. The windward Xiaodonghai fringing reef, however, is relatively less influenced by human activities and the corals are in good state.

Daya Bay (114°30′－114°51′E, and 22°30′－22°50′N) (Figure 1), located to the left of the Zhujiang River and southeast of Shenzhen City of Guangdong Province, is typical of subtropical ocean environment. The lowest monthly SST is 14－15℃, the highest monthly SST is 26－27.5℃, and the annual mean SST is 21－22℃. The Daya Bay is surrounded by hills and the discharging freshwater is mainly from streams and runoff. Coral communities are sporadically distributed in the Bay, but they have not developed into coral reef due to climate limitation. Many corals are found accreting to big rocks being about 10 m away from coast and about 4 m in water depths. Significant living coral cover decline was also observed in the latest ecological survey[25].

2 Materials and methods

Following the standard procedure[21,26−29], we analyzed the zooxanthellae population density (zooxanthellae mass per square centimeter) in the following steps: (1) Coral samples (with surface area of ~25−50 cm^2 each) were collected from Sanya Bay in April 2006 and from Daya Bay in June 2006, both around 4:00 pm, and then were immediately refrigerated for 2 h at temperature below 0℃. The top 1－2 cm of coral branches was removed as few zooxanthellae are present within these newly grown parts. (2) The samples were then sealed into a container and zooxanthellae were separated from coral skeletons using a high-pressure water jet (Water-Pik$^{\mathrm{TM}}$[21,26]) running on 0.45 μm filtered seawater. (3) The initial volume of the slurry was measured using a

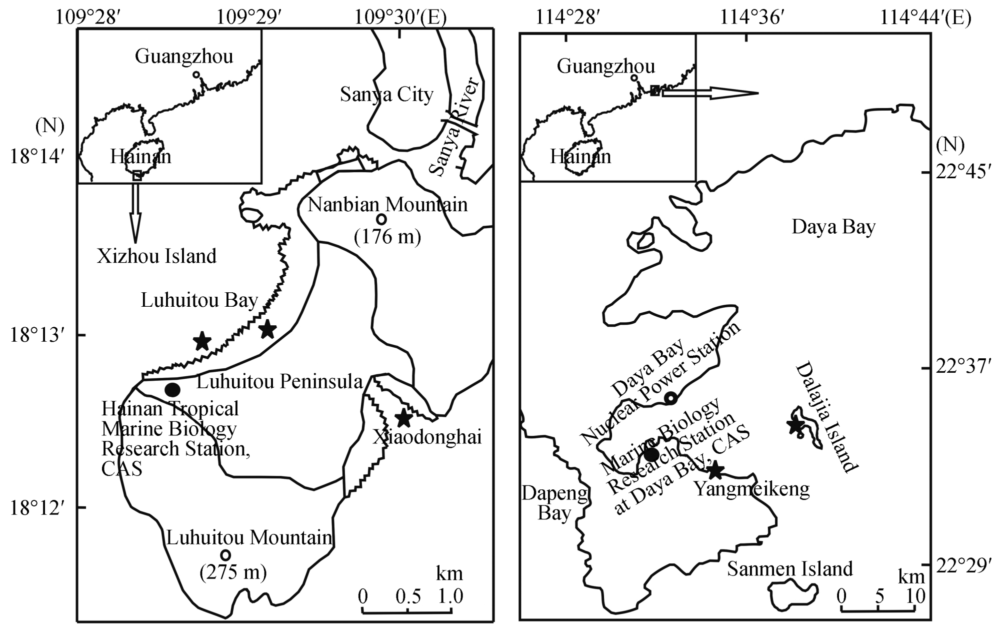

Figure 1 Study site (★) in Sanya of Hainan Island and Daya Bay of Guangdong Province.

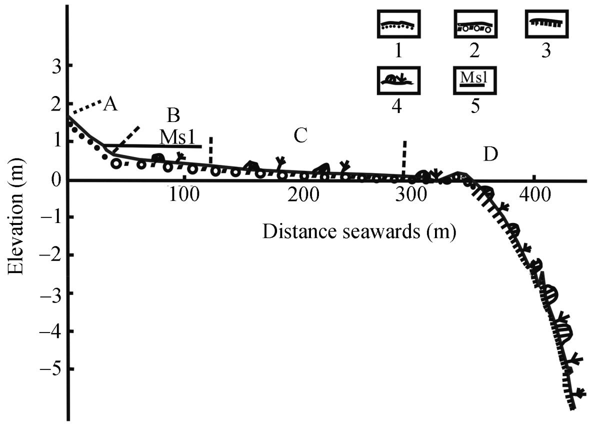

Figure 2 Geomorphologic pattern of fringing coral reefs in Sanya Bay (modified from ref. [23]. A, Sand beach; B, inner reef flat; C, outer reef flat; D, reef slope. 1, Biogenic sand; 2,coral sand and gravel; 3, *in situ* coral blocks; 4, living coral; 5, mean sea level.

measuring cylinder and recorded after cleaning twice the container. (4) After being thoroughly homogenized, the slurry was divided into 6 aliquots (each 3 mL), and was then centrifuged (RCF = 1062 g) for 3 minutes, the supernatant was discarded and the algal in residuum was preserved in 1 mL of 5% formaldehyde for 2 to 4 h at ~6℃ for further analysis. (5) Cell counts were measured by replicate hemacytometer counting (*n* = 10—12) under microscope. (6) The density of symbiotic zooxanthellae was calculated after determining the surface areas of coral skeletons using the relationship between the weight and surface area of the aluminum foil[27] used for wrapping the coral skeletons.

A total of 128 samples comprising 39 species of 21 genera collected from Luhuitou and Xiaodonghai of Sanya Bay and Daya Bay were analyzed and the results are listed in Table 1. The results show that the coral symbiotic zooxanthellae density ranges from 0.67×10^6 cell/cm^2 to 8.48×10^6 cell/cm^2.

3 Results and discussion

3.1 The interspecies variability in symbiotic zooxanthellae density

We measured zooxanthellae concentrations in corals from 10 species of 7 genera at 1—2 m from reef slope of Xiaodonghai reef (Figure 3(a)). The mean zooxanthellae density in these corals is ~2.54×10^6cell/cm^2, with *Pavona frondifera* having the lowest (1.39×10^6cell/cm^2) and *Porites lutea* the highest (3.95×10^6cell/cm^2). There is a discernible variation in zooxanthellae density among different coral genera. For instance, branching *Acropora* and *Pocillopora* have lower zooxanthellae density compared with massive *Porites*. Even within the same genus, symbiotic zooxanthellae density differs for different species, e.g., it is lower in *Porites andrewsi* than in *Porites lutea* and *Porites pukoensis* and higher in *Acropora pulchra* than in *Acropora hyacinthus* and is twice higher in *Pavona decussate* than in *Pavona frondifera*. Fitt et al.[21] concluded that zooxanhtellae levels in *A. palmate*

Table 1 The symbiotic zooxanthellae density in Scleractinian coral

Family	Genera	Species	Zooxanthellae density ($\times 10^6$ cells/cm^2)	Depth (m)	Colony form
Acroporidae	*Acropora*	*Acropora brueggemanni*	2.15±0.63	1—7	branching
		Acropora florida	1.89a)	6—7	branching
		Acropora formosa	0.67±0.26	6—7	branching
		Acropora humilis	1.95±0.35	1—4	branching
		Acropora hyacinthus	1.52±0.46	1—4	branching
		Acropora insignis	1.49±0.23	1—4	branching
		Acropora pulchra	2.23±0.03	3—4	branching
		Acropora robusta	2.03±0.85	1—2	branching
		Acropora solitaryensis	2.10±0.77	1—4	branching
	Montipora	*Montipora digitata*	2.47±0.49	1—4	branching
		Montipora solanderi	0.96	3—4	foliose
		Montipora turgescens	3.32	1—2	massive
Faviidae	*Cyphastrea*	*Cyphastrea serailia*	2.81±0.05	1—2	massive
	Favia	*Favia speciosa*	2.17	3—4	massive
	Favites	*Favites abdita*	5.83	1—2	massive
	Plesiastrea	*Plesiastrea versipora*	6.8±3.03	1—2	massive
	Echinopora	*Echinopora lamellosa*	2.22	1—2	foliose
	Goniastrea	*Goniastrea retiforms*	2.88	4—7	massive
		Goniastrea aspera	6.9±1.07	1—4	massive
		Goniastrea pectinata	1.92±0.48	1—7	massive
	Platygyra	*Platygyra daedalea*	5.49	1—2	massive
Oculinidae	*Galaxea*	*Galaxea astreata*	3.70±0.25	1—4	massive
Merulinidae	*Hydnophora*	*Hydnophora exesa*	3.24	1—2	encrusting
	Merulina	*Merulina ehrenberg*	1.75	1—2	foliose
Poritidae	*Goniopora*	*Goniopora duofasciata*	8.48±4.5	1—4	massive
	Porites	*Porites andrewsi*	2.14	1—2	submassive
		Porites lutea	3.74±1.5	1—7	massive
		Porites pukoensis	3.65	1—2	massive
		Porites rus	2.89±0.18	6—7	massive
Agariciidae	*Pavona*	*Pavona cactus*	1.78±0.36	4—7	foliose
		Pavona decussata	2.40±0.45	1—7	foliose
		Pavona frondifera	1.39±0.18	1—7	foliose
Pocilloporida	*Pocillopora*	*Pocillopora damicornis*	1.86±0.48	1—7	branching
		Pocillopora verrucosa	1.71±0.37	1—7	branching
Siderastreidae	*Psammocora*	*Psammocora contigua*	1.09	1—2	branching
Fungiidae	*Sandalolitha*	*Sandalolitha robusta*	1.7	3—4	massive, bleaching
Mussidae	*Symphyllia*	*Symdalolitha agaricia*	3.0±0.17	1—7	massive
Dendrophylliidae	*Turbinaria*	*Turbinaria peltata*	4.72±1.56	1—2	foliose
Helioporidaeb)	*Helioporade*	*Heliopora coerulea*	1.00±0.06	3—4	massive

a) represent one sample; b) means Helioporidae belongs to Coenothecalia, Octocorallia

are significantly higher than *A. cervicornis* at any depths and in any conditions; they are higher in *Montastrea faveolata* than in *Montastrea annularis* at the depths of 1—4 m, but show no difference between the two inter-general corals at a 13m-depth site. At different parts of the same colony, the loss rates of symbiotic zooxanthellae are different, with zooxanthellae density in the tips of *Acropora formosa* being lower than in the bottom of the skeleton[29].

Another feature is also quite notable, i.e. zooxanthellae density in massive species such as *Porites, Symphyllia, Galaxea* and *Turbinaria* is twice higher than in branching species such as *Acropora* and *Pocillopora*; this feature is clearly shown in the outer reef slope of Xiaodonghai (Figure 3(a)). This phenomenon is clear even within the same genera, e.g., branching coral *Montipora digitata* has a mean zooxanthellae density of 2.2×10^6 cells/cm^2, whereas at the same depth mass coral *Montipora turgescens* has a mean zooxanthellae level of 3.3×10^6 cell/cm^2.

Zooxanthellae density in 25 healthy coral species on the reef flat of Luhuitou (Figure 3(b)) shows that

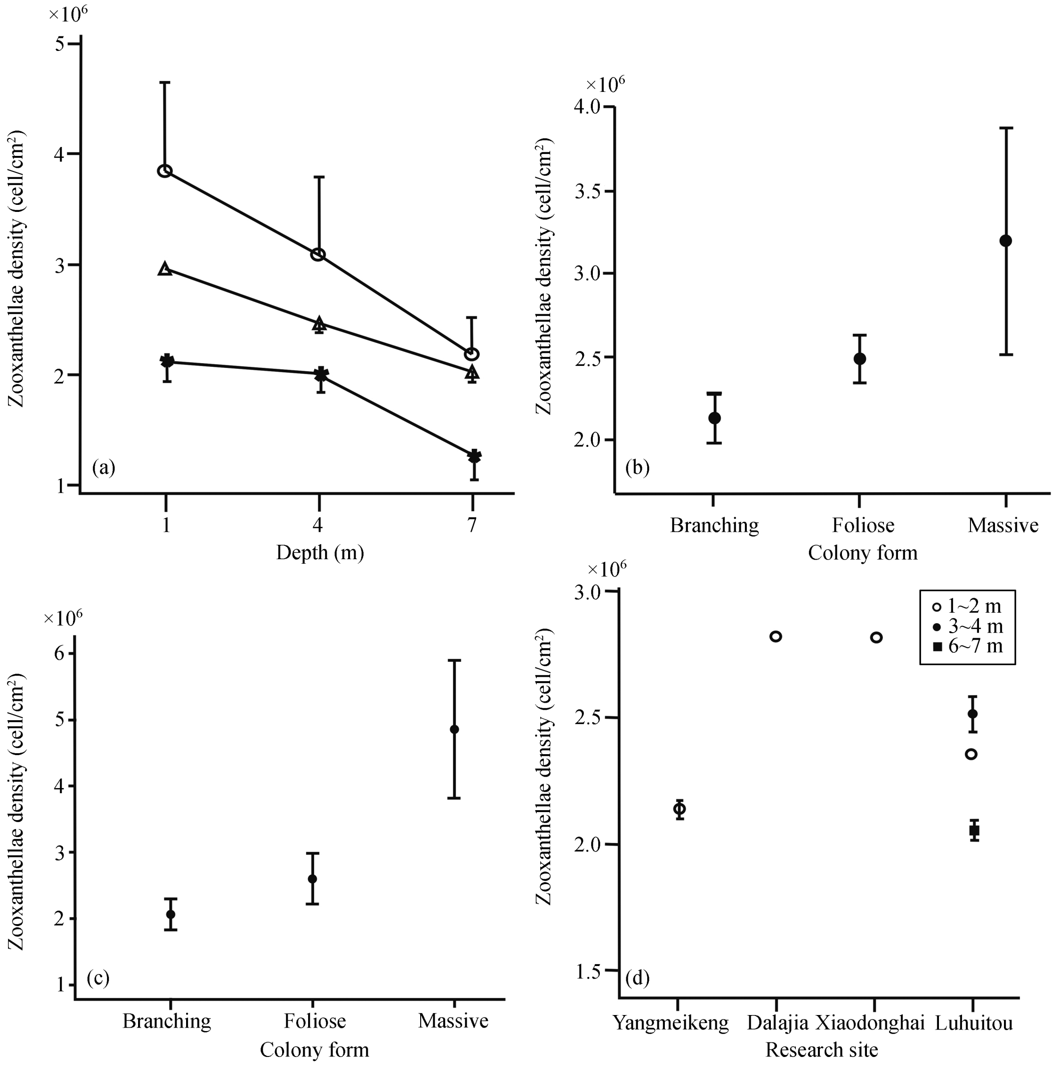

Figure 3 The distribution of zooxanthellae density. (a)Varieties of symbiotic zooanthellae density at different water depths at reef slope of Xiaodonghai in Sanya (★ branching species; Δ Foliose *Pavona decussate*; massive species); (b) distribution of symbiotic zooxanthellae density within different coral colony form at reef plate of Luhuitou in Sanya; (c) Zooxanthellae density within different colony form collected from Daya Bay; (d) symbiotic zooxanthellae density of *Pavona frondifera* at different sites. Error bars represent SE.

branching species have mean zooxanthellae density below 2.35×10^6 cells/cm^2, while massive species have significantly higher zooxanthellae density, with massive *Goniopora duofasciata* having the highest (11.8×10^6 cell/cm^2), 2—7 times higher than in branching coral species. These data indicate that zooxanthellae density in mass species is higher than in branching species, with foliose species being intervenient, which resembles the situation in Xiaodonghai (Figure 3(a)) and Daya Bay at higher latitudes (Figure 3(c)). It is worth noting that experimental results reported by Zhu et al.[30] have showed that symbiotic zooxanthellae loss rates differ significantly for different types of corals, with branching *Acropora* losing more symbiotic zooxanthellae than other corals under the same conditions.

Although coral reef bleaching was reported as early as in 1964[5], since 1983, this ecological phenomenon has attracted people's attention[31]. Based on surveys and comparative studies accumulated over the past two decades, it was found that coral reef bleaching shows a marked difference between different genera, e.g., Edwards et al.[32] reported that more than 98% *Acroporidae* and *Pocilloporidae* suffered bleaching and subsequent mortality on an artificial reef flat in Maldives in 1998, whereas massive species such as Poritidae, Faviidae and Agariciidae on the same reef flat survived that bleaching event. Stimson et al.[13] summarized coral bleaching phenomena observed in the entire Indian and Pacific

Oceans and ranked the coral genera in the order of decreasing vulnerability to bleaching as follows: *Acropora* > *Stylophora* > *Pocillopora* > *Montipora* > *Heliopora* > *Favia* > *Porites*, among which *Acropora*, *Stylophora and Pocillopora* species are all branching types, and the rest are massive corals. In addition, four branching species of the *Porites* genus (*P.silllimaniana, P.cylindrica, P.borizontalata* and *P. attenuata*) in Okinawa suffered severe bleaching and mortality in 1998, whereas massive colonies of the same genus at the same site (*P. lute*, *P. lobata*, *Goniastrea aspera*) survived and their relative abundance increased after the 1998 bleaching event[15]. McClanahan et al.[14] reported that *Acropora* and branching *Porites* species in the Great Barrier Reef were both moderately affected by bleaching, but those in Kenya were severely damaged. Comparing zooxanthellae data for corals in the northern South China Sea with the above reports, we speculate that there must be some inherent relationship between zooxanthellae and coral resistance to bleaching, with corals of high zooxanthellae levels being more resistant to bleaching. Warner et al.[33] suggested that higher zooxanthellae density may contribute to greater abundance of UV-absorbing compounds and thus play a self-protection role during bleaching event. The most susceptible *Pocillopora* corals have been found to have the least amount of UV-absorbing substances such as MAAs[34]. Leser et al.[35] reported a similar observation that shows that bleached corals often have less zooxanthellae and UV-absorbing compounds. Salih et al.[36] suggested that coral zooxanthellae density might be a measure of coral resistance to bleaching. Their study shows a significant correlation between coral resistance to bleaching and the concentration of fluorescent pigments in corals which are photo-protective.

3.2 Relationship between zooxanthellae density and water depth

The outer reef slopes (~7 m water depth) of Luhuitou and Xiaodonghai of Sanya feature the best-developed coral reefs. Systematic investigations of massive, branching and *Pavona decussate* corals collected from different depths (Figure 3(a)) show that zooxanthellae mean density declines with increasing water depths, with corals living at the bottom (6—7 m) having lower zooxanthellae density than those at 1—4 m water depths. However, no significant variations in zooxanthellae density were found in branching corals within 1—4 m depth probably due to sufficient photosynthesis in shallow water[37]. In a study of zooxanthellae density in Bahamas, Fitt et al. [21] also found that corals living in shallow water often have higher zooxanthellae levels compared to those in deep water. In addition, Warner et al.[37] also found that zooxanthellae photosynthetic Fv/Fm in reef-building coral genus *Montastrea* at 1—2 m depth show great seasonal fluctuations, with the highest occurring in winter, and the lowest in summer, whereas those in deeper waters (3—4 and 14 m depths) had consistently higher Fv/Fm. This observation indicates that branching corals are impressible when environmental conditions fluctuate. On the other hand, our study also shows that high turbidity may reduce zooxanthellae density. At our sampling site, the bottom of the sea is at 6—7 m depth, where suspended sediment concentrations are higher and water clarity is lower. At this level, the zooxanthellae density was found to be lower. A similar study by Costa et al.[38] showed that continental runoff affects water clarity and reduces the zooxanthellae density in *Montastrea cavernosa* corals in northeast Brazil. In addition, another study[27] demonstrated that frequent anthropogenic activity may modify environmental parameters such as dissolved oxygen, nitrate, phosphate concentrations and change zooxanthellae density in *Acropora formosa* corals. Recent research also suggests that high nutrition levels resulting from breed aquatics, and water pollution by terrestrial inputs and frequent diving are the main causes of coral ecological degradation in the study area [39,40]. Such causes may also reduce the zooxanthellae density. Further research is needed to clarify this.

3.3 Region diversity of symbiotic zooxanthellae density

In order to understand the regional diversity in zooxanthellae density, we collected *Pavona decussata* from Xiaodonghai and Luhuihou reefs in Sanya, which is in a tropical sea area, and Dalajia and Yangmeikeng in Daya Bay, which is in a subtropical sea area where corals have not formed reef. These two areas are 5° at latitude apart from each other. We chose different collection time to achieve the same SST approximately at 26℃. Zooxanthellae density varies within 2×10^6 — 3×10^6 cell/cm^2 at all four sites and shows no visible spatial variation (Figure 3(d)). For instance, the zooxanthellae density in Dalajia and Xiaodonghai is about 2.85×10^6 cell/cm^2, and that in Yangmeikeng and Luhuitou is $2\times10^6—2.5\times10^6$ cell/cm^2.

On the other hand, corals of the same genus in the same area show significant variability in their symbiotic zooxanthellae density. For instance, symbiotic zooxanthellae density in *Pavona decussata* corals in Xiaodonghai reef in Sanya is significantly higher than that at Luhuitou reef in Sanya. A similar difference was also observed between Dalajia and Yangmeikeng in Daya Bay. We attribute such observations to different levels of environmental impact. For instance, Luhuitou reef has been severely influenced by recent human activity and the corals there have experienced severe degradation[39]. By contrast, the less-impacted Xiaodonghai reef is much more healthy. Similarly, the observed difference between Dalajia and Yangmeikeng in Daya Bay should also be due to different degrees of environmental impact. For instance, Dalajia Island is an isolated island separated from the coast, and is less influenced by terrestrial input and human activity. By contrast, Yangmeikeng is adjacent to the coast where a large area has been leveled for road construction, and urchin breed aquatics are in the vicinity. Both processes may provide high levels of nutrients and contaminants that may impact on the zooxanthellae density in the corals. Ecological survey found there were many bleached or dead massive corals and no branching corals at ~1m depth in Yangmeikeng. Only a few branching species were found at 2—4 m depths. Wu and Wang[41] analyzed water quality data of the past 20 years from Daya Bay and found the atomic N: P ratio has increased continuously, and the nutrient structure has changed over the past 20 years, with ammonia and nitrate concentrations being the highest in summer. Nitrate-form nitrogen concentrations increase from east to west whereas phosphate levels are highest along the coast and lowest at the entrance to the bay. Based on such observations, we conclude that under the same climate conditions, water quality is the main aspect influencing the zooxanthellae concentrations. Studies by Wilkinson[3] and Lambo[42] suggested that the resilience of zooxanthellae to the 1998 bleaching event is affected by human activities, especially increased terrestrial input and sediment loads and related increase in turbidity, as well as over-farming and exploitation of coastal areas.

3.4 Differences in zooxanthellae density between bleached, semi-bleached and healthy corals

A partially-bleached *Plesiastrea versipora* coral was found in Yangmeikeng in Daya Bay (Figure 4a) and another partially-bleached *Sandalolitha robusta* coral was collected at Luhuitou in Sanya (Figure 4(b)), both located at ~ 1m water depth. We cut each sample into three parts: bleached, semi-bleached, and healthy-looking parts, respectively. A comparison of zooxanthellae densities within these parts shows that the loss rates of zooxanthellae in semi-bleached and bleached *Plesiastrea versipora* were 38.7% and 100%, respectively, whereas loss rates of zooxanthellae in semi-bleached and bleached *Sandalolitha robusta* were 39.6% and 99.4%, respectively (Figure 4(c)). Harithsa et al.[43] studied the stress response of the branching coral *A. Formosa* to the 2002 bleaching event in southwest India, and found that semi-bleached and bleached parts experienced a loss of zooxanthellae by more than 70% and 90%, respectively, higher than those of the massive coral species *P. lutea*, which are 20% and 78%, respectively. Brown et al.[44]

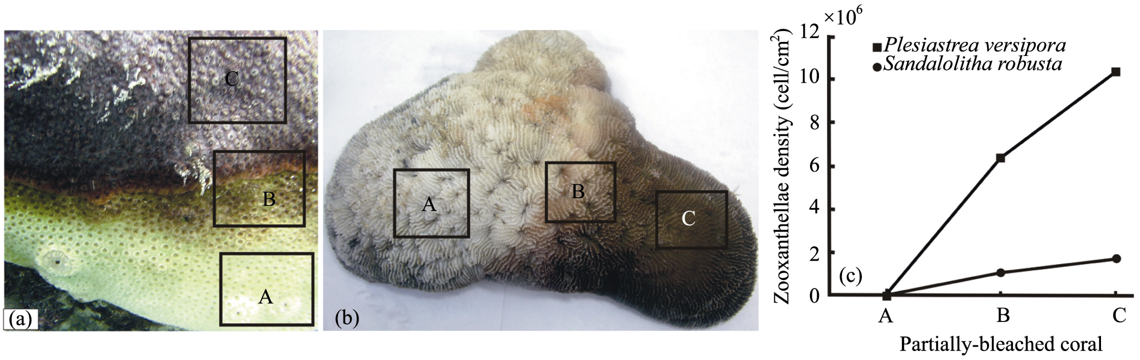

Figure 4 Differences of zooxanthellae density in partially-bleached corals. (a) *Plesiastrea versipora*; (b) *Sandalolitha robusta*; (c) Zooxanthellae density in partially-bleached corals. A, bleached; B, semi-bleached; C, healthy-looking.

studied bleaching response to five different species of massive corals showing that zooxanthellae loss varies between 50% and 90%, depending mainly on species. Thus it can be concluded that coral bleaching is closely related to the symbiotic zooxanthellae density. Even partially-bleached *Plesiastrea versipora* corals contain 2—3 times more zooxanthellae than healthy branching corals. This could be why branching corals are much more susceptible to bleaching than massive corals.

4 Conclusions

Using a universally-accepted method for measurement of symbiotic zooxanthellae density, we studied 128 samples comprising 39 coral species of 21 genera from Luhuitou and Xiaodonghai in Sanya at a lower latitude setting and Daya Bay at a higher latitude setting. The results show that:

(1) Mean zooxanthellae density varies from 0.67×10^6 to 8.48×10^6 cell/cm^2, displaying significant interspecies diversity, with the branching, foliose and massive species having the lowest(0.67×10^6—2.47×10^6 cell/cm^2), intermediate and highest(1.00×10^6—8.48×10^6 cell/cm^2) levels of zooxanthellae counts.

(2) Zooxanthellae density decreases with increasing water depth, with corals living in shallow water (~4 m) having significantly higher zooxanthellae density than that living at the sea floor (~7 m depth), which is probably related to levels of sunlight intensity and water clarity.

(3) Comparing sites from higher-latitude Daya Bay (~22°N) with those from lower-latitude Sanya (~18°N), the coral samples show similar symbiotic zooxanthellae density if they were collected at the same SST. However, significant variations in symbiotic zooxanthellae density exist among sites of the same latitude due to different local environmental conditions such as different levels of terrestrial inputs, sediment loads and turbidity, as well as different degrees of farming and development of coastal areas.

(4) In partially-bleached corals, zooxanthellae levels decrease from healthy-looking part, through semi-bleached part, to fully-bleached part, which suggests that coral bleaching has a close relationship with zooxanthellae density.

(5) Lower zooxanthellae density in branching species than in massive species is responsible for branching species being more susceptible to bleaching. For example, branching species *Acropora* and *Pocillopora* have lower zooxanthellae density than massive *Porites* and the formers are also more likely to be bleached and die compared with the latter.

The authors thank Dr. Chen Gang from Department of Marine and Fishery of Hainan Province for assistance during fieldwork. The Sanya National Coral Reef Natural Reserve, the Marine Biology Research Station at Daya Bay of CAS, and the Hainan Tropical Marine Biology Research Station of CAS provided support to the fieldwork.

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