

Coral symbiotic communities from different environments of an isolated atoll: reef lagoon versus forereef

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ABSTRACT: The variability of the species composition and community structure of coral ectosymbiotic invertebrates was studied using the reef-building coral *Pocillopora verrucosa* sampled from Dongsha Atoll (the northernmost atoll of the South China Sea). Overall, we discovered 61 symbiotic species, comprising 17 specialized obligate species and 44 generalists (facultative species and species with uncertain status). The total species richness, mean species number and mean abundance per colony were significantly higher in the lagoon than in the forereef, likely due to their respective temperature regimes. The lagoon is characterized by more frequent thermal anomalies than the forereef is, causing greater coral bleaching. This higher frequency of thermal stress apparently results in frequent renovations of coral-symbiotic communities following post-bleaching coral recovery, which seem to be associated with the increased diversity of commensal fauna and, particularly, with the abundance of facultative symbionts.

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KEY WORDS: coral-associated fauna, *Pocillopora*, Dongsha Atoll, South China Sea.

Отличия в структуре симбиотических сообществ, ассоциированных с кораллами из разных условий среды: пример с изолированного кораллового атолла

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РЕЗЮМЕ: В статье рассматривается изменчивость видового состава и структуры сообществ, ассоциированных с кораллами эктосимбиотических беспозвоночных на

примере рифообразующего коралла *Pocillopora verrucosa*. Исследования были проведены на атолле Донгша (самый северный атолл Южно-Китайского моря). Всего найден 61 вид эктосимбионтов из которых 17 видов были специализированные облигатные симбионты, а 44 вида — генералисты (факультативные симбионты + виды с неопределенным статусом). В лагуне, по сравнению с внешним рифом, было выше общее видовое богатство эктосимбионтов, а также среднее число видов и обилие эктосимбионтов на колонию, что вероятно может быть обусловлено существенными различиями в температурном режиме между этими рифовыми зонами. Лагуна характеризуется более частыми температурными аномалиями и обесцвечиванием (бличингом) кораллов по сравнению с внешним рифом. Такой более частый температурный стресс, по-видимому, повышает частоту обновления сообществ макросимбионтов после стадии бличинга коралла-хозяина, что в свою очередь способствует повышению их разнообразия и численности за счёт факультативных видов. Как цитировать эту статью: Tkachenko K.S., Soong K., Deart Y.V. Britayev T.A. 2022. Coral symbiotic communities from different environments of an isolated atoll: reef lagoon versus forereef // *Invert. Zool.* Vol.19. No.1. P.78–90. doi: 10.15298/invertzool.19.1.08

КЛЮЧЕВЫЕ СЛОВА: эктосимбионты кораллов, *Pocillopora*, атолл Донгша, Южно-Китайское море.

Introduction

Coral reef scleractinia, especially branching acroporids and pocilloporids, harbor a great diversity of associated symbiotic invertebrates and the topographic complexity of their three-dimensional structures generates a high variety of microhabitats (Stella *et al.*, 2010, 2011). Corals host numerous mutualistic ectosymbionts, mainly crustaceans that benefit from shelter, food, and reproductive facilities, provided by the hosts, while providing cleaning services, defense against predators and the mitigation of disease to their host corals (Stewart *et al.*, 2006, Stella *et al.*, 2010, 2011; Pollock *et al.*, 2012). Coral reefs are degrading worldwide due to climate change, anthropogenic impacts and biological disturbances (predator outbreaks and coral diseases) leading to habitat and food depletion, and major changes in the community structure, decreased fecundity and fitness of their associated symbionts, and the decline or even local extinction of highly specialized symbiotic species (Munday, 2004; Stella *et al.*, 2011).

The branching species of Acroporidae and Pocilloporidae are the most susceptible to the

effects of environmental disturbances, including thermal stress and related bleaching (Baird, Marshall, 2002; McClanahan *et al.*, 2004, 2007; Darling *et al.*, 2012). Among them, *Pocillopora* species harbor the highest proportion of coral symbionts (Stella *et al.*, 2011). At least 900 invertebrate species are known to be associated with 44 coral taxa; of these, approximately 250 are associated with *Pocillopora* (Stella *et al.*, 2011). Most coral-associated invertebrates are highly dependent on their living hosts and, exhibit a clear preference for those more susceptible to bleaching and mortality (Pratchett *et al.*, 2009; Stella *et al.*, 2011). Therefore, extinction rates of these species will likely increase due to fitness decline and subsequent population decline if reefs continue to degrade at the present rates.

Pocillopora species exhibit significant geographic variability in the species composition of their symbiotic communities, which is mainly caused by changes in facultative symbionts and species with uncertain status (SUS), whereas the obligate components of their communities seem to be more stable (Stella *et al.*, 2010, 2011; Britayev *et al.*, 2017). The effect of local (habitat) variability and environmental conditions

on the composition and structure of these symbiotic communities is still poorly understood, although greater differences in environmental parameters may be observed within the same coral reef (Edwards, Emberton, 1980; Black, Prince, 1983).

The aims of this study were to assess the local variability in the species composition and structure of coral-associated symbiotic communities and to determine whether they differ between the reef lagoon and the forereef, which are exposed to different temperature regimes and wave exposure. Accordingly, we examined the species composition, species richness and abundance of three categories of species (obligate and facultative macrosymbionts and SUS) living in association with the coral *Pocillopora verrucosa* (Ellis et Solander, 1786) in the forereef and lagoon of an isolated atoll (Dongsha Atoll of the South China Sea).

Material and methods

STUDY AREA AND SAMPLING DESIGN. Dongsha Atoll (also known as the Pratas Islands), the northernmost atoll in the South China Sea, is a nearly circular reef of approximately 25 km in diameter that suffered a catastrophic coral mortality (>90% of cover) in its lagoon during the severe elevated sea surface temperature (SST) anomaly in 1998 (Dai, 2006). During the following years, the atoll suffered SST elevations almost every year (18 events vs. 6 normal years without elevations) (Tkachenko, Soong, 2017; https://coralreefwatch.noaa.gov/product/vs/timeseries/east_asia.php#dongsha). The most pronounced anomalies occurred in 2007, 2010, 2014–2016, 2019–2021, when the degree heating weeks (DHWs) exceeded the bleaching alert level (DHWs>8). At the same time, the coral cover on the outer reef slopes (forereef) remained high and virtually undamaged, which may be explained by the episodic upwelling of deep waters due to internal gravity waves (Dai, 2006). Dongsha Atoll is located in the Luzon Strait, a passage zone with the world's strongest known internal waves generated by barotropic tides, which may reach a height of

200 m and velocity amplitude of 0.3 m s^{-1} within approximately 4 h period (Wang *et al.*, 2007). These internal waves cause daily abrupt temperature decreases of up to $8 \text{ }^{\circ}\text{C}$ in the forereef, consequently buffering coral communities from heat-induced bleaching (Wang *et al.*, 2007; DeCarlo *et al.*, 2015, 2017). These unique hydrological features contributed to the significant differences in coral species composition and abundance between the lagoon and the forereef, which is considered a potential thermal refuge for the reef-building corals of the northern South China Sea (Tkachenko, Soong, 2017). The forereef is exposed to lower seawater temperature means, maximums, and minimums than the lagoon is (mean $24.2 \pm 2.7 \text{ }^{\circ}\text{C}$, range $17.5\text{--}30.5 \text{ }^{\circ}\text{C}$ and mean $26.3 \pm 3.8 \text{ }^{\circ}\text{C}$, range $19\text{--}31.8 \text{ }^{\circ}\text{C}$, respectively). To monitor these differences in thermal regime, two HOBO temperature loggers (HOBO U22-001, Onset, Bourne, MA, USA) were deployed at a 10-m depth in both reef zones in the vicinity of sampling sites for 1 year (September 9, 2019, to August 24, 2020), and the temperature was recorded four times a day. In addition, the open forereef was considered a priori to face higher wind and wave load than the enclosed lagoon, which was protected from wave exposure coming from open sea by the atoll coral rim.

The sampling of colonies of *P. verrucosa* was performed in two geomorphic reef zones (Fig. 1): (1) the reef lagoon (the northern reef of Dongsha Island, the only above-water island of the atoll at $20^{\circ}42'48''\text{N}$, $116^{\circ}4'57''\text{E}$) in June 2016 and July 2019 (20 colonies), and (2) the forereef (the eastern reef of Dongsha Atoll at $20^{\circ}44'50''\text{N}$, $116^{\circ}54'27''\text{E}$) in August 2014 and July 2019 (24 colonies). The colonies were collected by SCUBA diving at a 3- to 7-m depth and were identified according to Veron (2000). Each individual healthy and normally colored coral colony was covered with a fine mesh net to prevent animals from escaping, carefully detached from the substrate and placed in an individual bucket of fresh filtered seawater for inspection in a coastal laboratory at Dongsha Atoll Research Station. Each colony was photographed and measured (maximum and perpen-

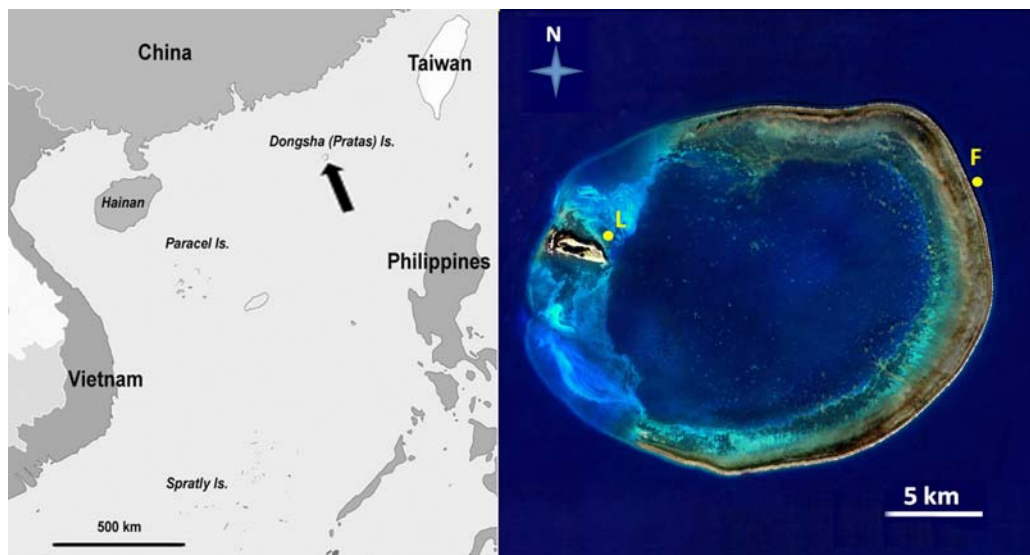


Fig. 1. Dongsha Atoll. Left: location in the South China Sea. Right: study sites. Abbreviations: L — lagoon; F — foreereef.

Рис. 1. Атолл Донгша. Слева: расположение атолла в Южно-Китайском море. Справа: станции сбора проб. Обозначения: L — лагуна; F — внешний рифовый склон.

dicular diameters and height) to estimate the volume. Then, each colony was submerged for 3 min in an emulsion of 0.5 mL of clove oil in 1000 mL of filtered seawater to anesthetize the symbiotic fauna, which allowed us to remove the visible animals using blunt probes and forceps. Then, all the colonies were intensively washed with the clove oil and seawater emulsion and the obtained solution was poured through a 1×1-mm pore net to retain the invertebrates. Boring invertebrates and animals smaller than 1 mm were not considered. All the associated invertebrates were photographed and preserved in 70% or 96% alcohol for further processing. The processed colonies of *Pocillopora* were returned to the original reef and attached to a stable natural substrate using plastic lockers. Each individual invertebrate was identified to the lowest possible taxonomic level based on specialized literature. The specimens with uncertain affiliation were identified at higher taxonomic levels (i.e., as polychaetes, amphipods, gastropods and bivalves) and counted to obtain the total abundance (i.e., the number of individuals per colony).

DATA ANALYSIS. All the specimens associated with the colonies of *Pocillopora* were divided into three main groups, namely obligate symbionts, facultative symbionts, and SUS (Stella *et al.*, 2011; Britayev *et al.*, 2017) to compare their diversity, mean abundance, and mean species richness per colony in the lagoon and the foreereef using non-parametric Kruskal–Wallis analysis of variance (K-WA) and parametric analysis of covariance (ANCOVA). For the purposes of our study, facultative symbionts and SUS were combined in a category named “generalists”. ANCOVA was used to assess the effect of the coral colony volume (as a covariate) on the differences between the two study sites. All analyses were performed using Statistica 8.0 for Windows (StatSoft, 2007).

Results

ENVIRONMENTAL PARAMETERS. The most pronounced differences between the study sites were caused by temperature regimes (Fig. 2), with the foreereef exhibiting higher variability and lower monthly mean and minimum tem-

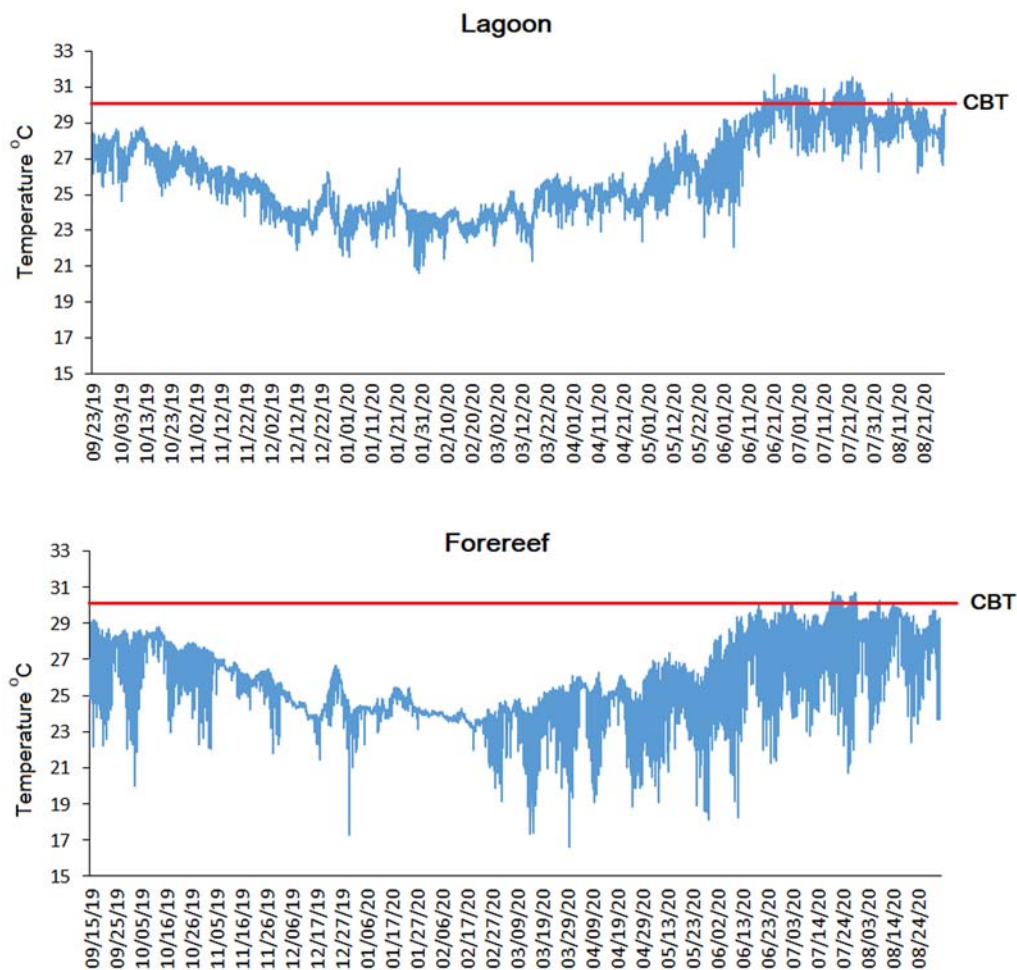


Fig. 2. Temperature dynamics in Dongsha Atoll from 2019 to 2020. Top: lagoon; bottom: foreereef; red line: coral bleaching threshold.

Рис. 2. Температурная динамика придонного водного слоя в период 2019–2020 на станциях в лагуне (верхний рисунок) и на внешнем рифе (нижний рисунок); красная линия — температурный порог обесцвечивания (бличинга) кораллов.

peratures than the lagoon, leading to an almost negligible excess of the coral bleaching threshold. In the hottest period of 2020 (mid-June to mid-July), the mean temperature of the lagoon study site was 29.6 °C (range 27.1–31.7 °C) and DHWs reached 3 °C per week, whereas the mean temperature of the foreereef study was 27.6 °C (range 21.2–30.1 °C) and DHWs did not reach 1 °C per week, which caused less heat stress than that in the lagoon.

CORAL-SYMBIOTIC FAUNA. At Dongsha Atoll, 61 pocilloporid-associated taxa (Table 1) comprising 17 specialized obligate species and 44 generalists were discovered, the following trends were observed between the lagoon and the fore reef (Table 2):

1. The total species diversity was higher in the lagoon (49 species) than in the foreereef (33 species).

2. The ratio of obligate species to generalists

Table 1. List of symbiotic taxa associated with *Pocillopora verrucosa* at Dongsha Atoll.
 Таблица 1. Список таксонов симбионтов, ассоциированных с кораллом *Pocillopora verrucosa* с атолла Донгша.

NN	Taxa	Lagoon	Forereef
	Polychaeta		
1*	Polynoidae sp.	+	
2**	Eunicidae sp.		+
3*	Amparetidae sp.	+	
4*	Nereidae sp.	+	
5**	Phyllodocidae sp.		+
6*	Polychaeta sp.	+	
	Bivalvia		
7	<i>Lithophaga lessepsiana</i>	+	+
8*	Arcidae sp.	+	
9*	Pteriidae sp.	+	
10**	Gastropoda sp.		+
11*	<i>Mitrella</i> sp.	+	
12*	Triviidae sp.	+	
13	<i>Coralioophylla (Quoyula) monodonta</i>	+	+
14**	<i>Drupella cornus</i>		+
15**	<i>Drupa ricina</i>		+
16**	<i>Lima</i> sp.		+
17**	<i>Turbo</i> sp.		+
18*	<i>Pisania ignea</i>	+	
19*	Bivalvia sp.	+	
	Crustacea		
	Decapoda		
20	<i>Trapezia septata</i>	+	+
21	<i>Trapezia lutea</i>	+	+
22	<i>Trapezia digitalis</i>	+	+
23	<i>Trapezia bidentata</i>	+	+
24	<i>Trapezia guttata</i>	+	+
25	<i>Trapezia tigrina</i>	+	+
26*	<i>Trapezia cymodoce</i>	+	
26*	<i>Trapezia serenei</i>	+	
28	Majidae sp.	+	+
29*	<i>Domecia hispida</i>	+	
30**	<i>Cymo deplanatus</i>		+
31*	<i>Cymo</i> sp.	+	
32*	<i>Brachyura</i> sp.	+	
33	<i>Alpheus lottini</i>	+	+
34*	<i>Synalpheus charon</i>	+	
35	Alpheidae gen. sp.1	+	+
36	Alpheidae gen. sp.2	+	+
37*	Alpheidae gen. sp.3	+	
38	<i>Harpiliopsis beupressii</i>	+	+
39	<i>Harpiliopsis depressa</i>	+	+

Table 1 (continued).
Таблица 1 (продолжение).

NN	Taxa	Lagoon	Forereef
40**	<i>Harpillopsis spinigera</i>		+
41*	Palaemonidae sp.	+	
42*	<u><i>Hapalocarcinus marsupialis</i></u>	+	
43*	Galatheidae sp.1	+	
44**	Porcellanidae sp.1		+
45**	<i>Pisidia dispar</i>		+
46**	<i>Pachycheles sculptus</i>		+
47	Paguridae sp.1	+	+
48	<i>Calcinus minuthus</i>	+	+
49	<i>Calcinus vachoni</i>	+	+
	Stomatopoda		
50*	Stomatopoda sp.	+	
	Amphipoda		
51*	Amphipoda sp.	+	
	Ophiuroidea		
52	<i>Ophiocoma pica</i>	+	+
53	<i>Ophiactis savignyi</i>	+	+
54	<i>Ophiothrix trilineata</i>	+	+
55*	Ophiuroidea sp.	+	
	Pisces		
56	<u><i>Paragobiodon modestus</i></u>	+	+
57*	<u><i>Paragobiodon xanthosoma</i></u>	+	
	Demospongiae		
58*	Demospongiae sp. 1	+	
	Ascidiacea		
59*	Ascidiacea sp. 1	+	
60*	Ascidiacea sp. 2	+	
	Actiniaria		
61*	Actinaria sp.	+	

Obligate species are underlined.

* Found only in the lagoon

** Found only on the forereef

was slightly higher in the forereef (0.57) than in the lagoon (0.48).

3. In total, 20 shared species were discovered (11 obligate and 8 generalists), 28 species were discovered in the lagoon (5 obligate, 23 generalists,) and 12 were discovered only in the forereef (1 obligate, 11 generalists).

4. The mean species number and abundance

were positively correlated with the colony volume in both the lagoon and the forereef (Fig. 3), but were significantly higher in the lagoon with (ANCOVA) and without (K-WA) volume as a covariate (Table 2);

5. No significant differences were observed between the two reef zones in terms of the average species number or the abundance of

Table 2 Differences between symbiotic communities associated with *Pocillopora verrucosa* in the lagoon and the foreereef of Dongsha Atoll.
Таблица 2. Отличия между сообществами эктосимбионтов из лагуны и с внешнего склона атолла Донгша.

	Lagoon	Foreereef	K-WA/ANCOVA values
Number of pocilloporid colonies (n)	20	24	-
Mean colony volume (cm ³)	1074	1787	-
Total species number	49	33	-
Total number of obligate species	16	12	-
Total number of generalist species	33	21	-
Mean number of species per colony	9.3	6.3	K-WA: H = 7.23, p = 0.007*; ANCOVA: F = 4.3, p = 0.044*
Mean number of individuals per colony	17	12.2	K-WA: H = 5.75, p = 0.016*; ANCOVA: F = 5.13, F = 0.028*
Mean number of obligate species per colony	4.9	3.8	K-WA: H = 3.53, p = 0.060; ANCOVA: F = 3.08, p = 0.086
Mean number of generalist species per colony	4.2	2,4	K-WA: H = 5.72, p = 0.016*; ANCOVA: F = 3.89, p = 0.055
Mean number of obligate individuals per colony	8.9	8.4	K-WA: H = 1.4, p = 0.235; ANCOVA: F = 5.05, p = 0.029*
Mean number of generalist individuals per colony	8.1	2.3	K-WA: H = 7.28, p = 0.007*; ANCOVA: F = 4.38, p = 0.042*
Most common species (infestation rate)	<i>Alpheus lottini</i> (80%) <i>Trapezia bidentata</i> (70%) <i>Trapezia septata</i> (65%)	<i>Trapezia bidentata</i> (83%) <i>Trapezia septata</i> (71%) <i>Trapezia lutea</i> (54%)	

H and p values are based on non-parametric Kruskal-Wallis analysis of variance (K-WA); F and p values based on parametric analysis of covariance (ANCOVA) with colony volume as covariate.

*Significant difference

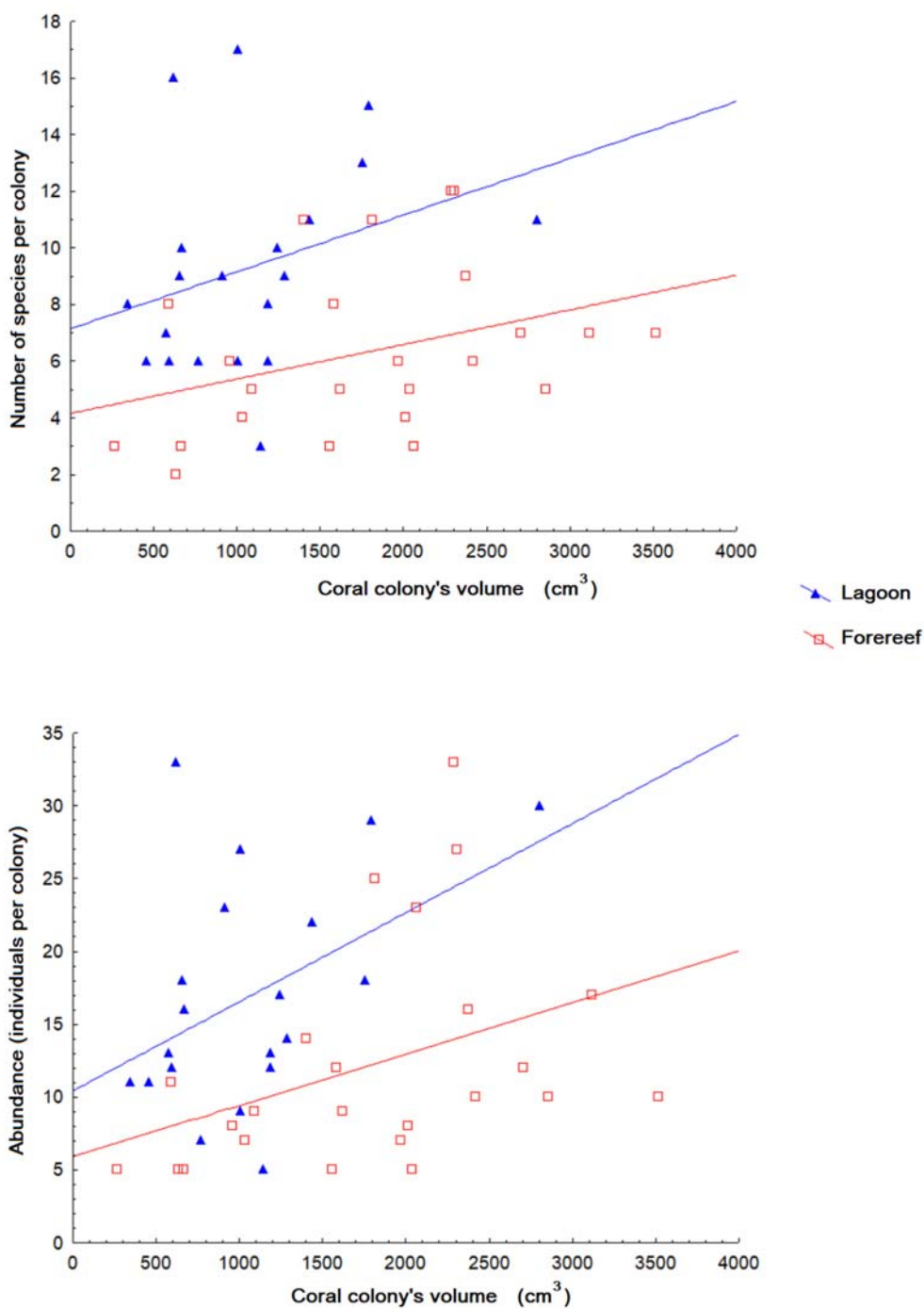


Fig. 3. Relationships between colony volume and symbiont species richness (top) and abundance (bottom) in the lagoon and forereef of Dongsha Atoll.

Рис. 3. Зависимости видового богатства (верхний рисунок) и обилия (числа особей) эктосимбионтов (нижний рисунок) от объема колонии.

obligate symbionts per coral colony (K-WA), although the abundance was correlated with the colony volume in both zones (ANCOVA, Table 2);

6. The mean species number and abundance of generalists were significantly higher in the lagoon than in the forereef, both with (ANCOVA) and without (K-WA) volume as a covariate (Table 2);

7. *Alpheus lottini* was dominant in the lagoon, whereas *Trapezia bidentata* was dominant in the forereef.

Discussion

The environmental parameters affecting the species composition and community structure of symbionts associated with corals are still not been thoroughly studied, but thermal stress triggering coral bleaching and wave exposure are among the most crucial (Munday, 2004; Stella *et al.*, 2011b). In this study we did not consider wave exposure due to the lack of relevant published data and our inability to monitor this parameter during the study period. However, Rogers *et al.* (2016) reported that wave stress models indicated a strong effect on the coral cover on atoll forereefs, and that locations exhibiting high stress were associated with a lower coral cover. According to our personal observations at the study sites, we suggest that the effect of wave exposure on the symbiotic coral communities contributed to the lower total abundance and species richness of symbionts observed in the forereef.

SST elevations triggering coral bleaching result in the following: (1) changes in the species composition of symbiotic fauna; (2) decline in the species richness and fecundity of obligate symbionts and an increase in the abundance of facultative symbionts; (3) shifts in sex ratio, with the male abundance becoming higher than that of females, and (4) increased competition in the symbiotic crustacean community and the outcompetition of shrimps by crabs (Stella *et al.*, 2011; Stella, 2015).

Many invertebrate symbionts are more sensitive to environmental changes than their host

corals are, and often experience mass mortality after acute disturbances (Tsuchiya *et al.*, 1992; Stella *et al.*, 2014). Moreover, the species richness and abundance of symbionts depend on amount of available living healthy host tissue, as bleached tissues produce less mucus (which is used as food by many symbionts) and are more prone to disease due to thermal stress (Brodnicke *et al.*, 2019) compared with healthy coral. In *Pocillopora damicornis* (Linnaeus, 1758), for example, bleaching may extend for over 1 month and kill only 10% of the colonies but cause much higher mortality in of symbiotic shrimps (75%) and crabs (33%) (Stella *et al.*, 2014).

As the lagoon of Dongsha Atoll is exposed to more pronounced and frequent temperature stress, and the forereef is protected by internal wave upwelling episodes, we initially assumed that the lagoon would host less diverse and less abundant symbiotic fauna. However, our results refuted this assumption, which may be partly attributed to the effect of wave exposure on coral-associated symbiotic communities in the forereef. Moreover, the higher frequency and severity of the episodes of thermal stress in the lagoon may result in a fast turnover of coral-associated fauna, leading to a high variability in both species composition and abundance. Hence, even as one of the main environmental factors negatively affecting coral reefs, increased frequency of exposure to sublethal temperatures may benefit the coral ectosymbiotic assemblages (provided that coral hosts survive anomalies), leading to increased abundance, species richness and diversity especially of facultative and SUS species. In addition, due to differential sensitivity to stress in the recovered communities, some of the most sensitive obligate symbionts may even be present in higher numbers than are their non-obligate competitors, as suggested by the prevalence of two dominant obligate crustaceans in the lagoon assemblage.

Thermal stress and coral bleaching in pocilloporids cause symbiotic crabs to outcompete symbiotic shrimps (Stella *et al.*, 2011). Moreover, the species of *Trapezia* and *Alpheus lottini* (Guérin, 1830), the most common symbiotic

taxa among *Pocillopora*-associated communities, are highly sensitive to coral bleaching and tend to escape from bleached colonies (Tsuchiya *et al.*, 1992). However, the obligate symbionts of the genus *Trapezia* may occur with either low densities on partially bleached colonies of *P. damicornis* (Glynn *et al.*, 1985) or increased in abundance after bleaching (Tsuchiya *et al.*, 1992). In this study, we found that the abundance of *A. lottini* in the lagoon, affected by frequent SST elevations, was higher than that in the forereef, which reflects the healthy state of lagoon's *Pocillopora*-associated communities.

Partial coral mortality (40–60% of live tissue) yielded the highest diversity and abundance of both obligate and facultative coral dwellers (Stella, 2015). The highest overall diversity occurred after intermediate colony mortality (20–80% of live tissue), presumably coinciding with a more heterogeneous microhabitat consisting of live coral tissue and various other substrates, such as algal turfs and sponges (Britayev *et al.*, 2017). The effects of coral disturbance on invertebrate species depend on the severity of the disturbance and the degree of habitat specialization, with moderate disturbances promoting invertebrate biodiversity and increasing spatial heterogeneity (Pratchett *et al.*, 2011; Stella, 2015). Positive associations have been observed between habitat diversity and species richness; moderate levels of disturbance may exert a negligible or even positive effect on local diversity (Pratchett *et al.*, 2011; Tews *et al.*, 2004; Hortal *et al.*, 2009). Different coral species support distinct assemblages of obligate associates when alive; however, once dead, they support overlapping communities of facultative and SUS species (Stella, 2015). As their diversity and abundance are higher than those of obligate species, the total diversity increases. Obligate species tend to occur in stable environments, whereas generalists often dominate disturbed environments (Devictor *et al.*, 2008; Clavel *et al.*, 2010). Overall, species richness peaks after intermediate disturbances (e.g., partial coral bleaching), whereas the lowest species richness occurs at 0 or 100% of healthy coral tissue

(Stella, 2015). Our data are partly consistent with this hypothesis: the abundance and species number of generalists (and, thus, the total diversity of symbionts) were significantly higher on lagoon coral colonies that experienced greater disturbances than those in the forereef. Accordingly, reefs maintaining equilibrium between healthy, unhealthy, and dead coral colonies may represent the best environment for maintaining the high biodiversity of cryptic invertebrates acting as coral symbionts.

Conclusions

Many studies have focused on snapshot responses of coral symbiotic communities to thermal anomalies and the associated stress triggering coral bleaching, whereas the long-term effects of periodic anomalies have seldom been considered. Our study demonstrated that a higher frequency and severity of thermal stress may result in a faster turnover and higher variability of coral-associated symbiotic communities in terms of both species composition and abundance. The symbionts associated with the pocilloporids of Dongsha Atoll exhibited lower diversity, species richness and abundance per colony in the forereef than in the lagoon, which was subjected to more frequent thermal anomalies triggering coral bleaching. Our data suggest that the higher frequency and severity of the episodes of thermal stress in the lagoon may result in a faster turnover of the symbiotic community after post-bleaching recovery, preventing specialized species from monopolizing hosts, which, in turn, leads to an increase in the diversity and abundance of the symbiotic fauna.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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