



Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Baseline

Stable Symbiodiniaceae composition in three coral species during the 2017 natural bleaching event in subtropical Hong Kong

Jack Chi-Ho Ip^{a,b,c}, Yanjie Zhang^d, James Y. Xie^a, Yip Hung Yeung^a, Jian-Wen Qiu^{a,b,c,*}^a Department of Biology, Hong Kong Baptist University, Hong Kong, China^b Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangzhou 511458, China^c HKBU Institute of Research and Continuing Education, Virtual University Park, Shenzhen, China^d School of Life Sciences, Hainan University, Haikou, China

ARTICLE INFO

Keywords:

Coral bleaching
Heatwave
ITS2 sequencing
Ocean warming
Subtropical corals
Symbiodiniaceae diversity

ABSTRACT

Adaptive changes in endosymbiotic Symbiodiniaceae communities have been reported during and after bleaching events in tropical coral species, but little is known about such shifts in subtropical species. Here we examined the Symbiodiniaceae communities in three coral species (*Montipora peltiformis*, *Pavona decussata*, and *Platygyra carnosa*) based on samples collected during and after the 2017 bleaching event in subtropical Hong Kong waters. In all of the collected samples, ITS2 meta-sequencing revealed that *P. decussata* and *P. carnosa* were predominantly associated with *Cladocopium* C1 and C1c, whereas *M. peltiformis* was mainly associated with two *Cladocopium* C21 types and C1. For each species, the predominant endosymbionts exhibited high fidelity, and the relatively low abundance ITS2-types showed minor changes between the bleached and recovered corals. Our study provided the first details of coral-algal association in Hong Kong waters, suggesting the selection of certain genotypes as a potential adaptive mechanism to the marginal environmental conditions.

The symbiotic relationship with the dinoflagellate family Symbiodiniaceae allows many scleractinian corals to have access to the photosynthates produced by the algae, and thus thrive in shallow tropical and subtropical waters (Hoegh-Guldberg, 1999). However, this symbiosis is sensitive to seawater temperature changes – a prolonged exposure to 1–2 °C above the average summer temperature maximum can result in bleaching – a breakdown of the symbiosis that reduces the algal density and produces the whitish bleaching phenotype (Goreau et al., 2000). During the last half-century, large-scale abnormal seawater warming has triggered several regional to global scale coral bleaching events, including those that occurred during 1982–1983 (Glynn, 1991), 1997–1998 (Wilkinson, 1998), 2010 (Alemu and Clement, 2014), and 2014–2017 (Eakin et al., 2019). As the seawater temperature is predicted to continually increase and there will be more heatwaves in this century (IPCC, 2014), understanding the coral-algal symbiosis and how such symbiosis responds to extreme environmental conditions are fundamental to predicting the future of coral reef ecosystems.

The family Symbiodiniaceae comprises the genera *Symbiodinium*, *Breviolum*, *Cladocopium*, *Durusdinium*, *Effrenium*, *Fugacium*, *Freudenthalidium*, *Gerakladium*, *Hallaxium*, Clade I, and Clade J (LaJeunesse et al., 2018; Yorifuji et al., 2021). Among these genera, the former four are

common symbionts of scleractinian corals. The genetic diversity of a coral's endosymbiont reflects its stress tolerance due to the differential photosynthetic efficiencies and environmental tolerance of Symbiodiniaceae genotypes (Baker, 2003; Pochon and Gates, 2010; Russnak et al., 2021). In general, coral colonies that host the stress-tolerant *Durusdinium* have a 1–2 °C higher thermal tolerance threshold than those that are associated with other genotypes such as *Cladocopium* (Mostafavi et al., 2007; Silverstein et al., 2015; Fuller et al., 2020). Some corals exhibit flexibility in their endosymbiont communities (e.g., shifting the algal partner from *Cladocopium* dominant to *Durusdinium* dominant during bleaching event (Ziegler et al., 2017; Gong et al., 2018; Gardner et al., 2019; Claar et al., 2020). However, even within *Cladocopium*, the sensitivity to thermal stress varies with genotypes (Hume et al., 2016), and certain coral species or populations still maintain highly stable symbiont communities over broad temperature gradients and through bleaching events (LaJeunesse et al., 2004; Smith et al., 2017; Osman et al., 2020; Voolstra et al., 2021). Therefore, for many coral species, especially those in subtropical regions that are less well-studied than tropical corals (Beger et al., 2014; Sully et al., 2019; Eddy et al., 2021), there is an urgent need to analyze the composition of Symbiodiniaceae community and its changes in response to extreme climate conditions.

* Corresponding author at: Department of Biology, Hong Kong Baptist University, Hong Kong, China.

E-mail address: qiuwj@hkbu.edu.hk (J.-W. Qiu).

<https://doi.org/10.1016/j.marpolbul.2022.114224>

Received 29 August 2022; Received in revised form 29 September 2022; Accepted 3 October 2022

Available online 11 October 2022

0025-326X/© 2022 Elsevier Ltd. All rights reserved.

Located in a subtropical environment with strong seasonal fluctuations in seawater temperature from 14 to 31 °C and a strong gradient of water quality due to the presence of the Pearl River Estuary to the west, Hong Kong's marine waters represent a marginal environment for coral reef development. Even in the eastern oceanic waters where coral communities are better developed, they typically grow on volcanic rocks as non-reefal colonies and are restricted to shallow waters <10 m deep (Morton and Morton, 1983; Yeung et al., 2021). A total of 84 scleractinian corals have been recorded in Hong Kong (Chan et al., 2005). Previous studies have found that these corals harbor a low diversity of Symbiodiniaceae, with the majority being *Cladocopium* genotypes (Ng and Ang, 2016; Wong et al., 2016; Saad et al., 2021). Despite being located in a subtropical environment, Hong Kong's coral communities have been affected by three bleaching events that occurred in the summers of 1997–1998 (McCorry, 2002), 2014 (Xie et al., 2017), and 2017 (Xie et al., 2020). However, no investigation has been conducted to understand the endosymbiont compositional changes during natural bleaching events in Hong Kong, or any of the fringing coral communities widely distributed along the coasts of the neighboring Guangdong Province of mainland China (Zhao et al., 2022).

In this study, we examined the endosymbiotic dinoflagellates communities associated with three common coral species in Hong Kong (Yeung et al., 2021), including *Montipora peltiformis*, *Pavona decussata*, and *Platygyra carnosa* (Fig. 1), based on samples collected during the 2017 heatwave. These selected species exhibited contrasting patterns of loss and recovery of algal symbiont/pigmentation indicating their differential bleaching susceptibility (Xie et al., 2020; Ip et al., 2022; Zhang et al., 2022). We compared the endosymbiont communities using high

throughput metabarcoding in coral samples collected from colonies with differential bleaching phenotypes (non-bleached and bleached) during the bleaching event (sampled in Jun-Aug 2017), as well as the same colonies (bleached) that have recovered from the bleaching event (sampled in Sep 2017; details in Supplementary Fig. S1). The results will improve our understanding of Symbiodiniaceae diversity in subtropical coral species, and form a baseline for monitoring Symbiodiniaceae community structure in the future.

We collected samples of *M. peltiformis*, *P. decussata*, and *P. carnosa* by SCUBA at 2–4 m water depth from Bluff Island (22°19'27.6"N 114°21'14.0"E), Sharp Island (22°21'54.3"N, 114°17'20.3"E), and Lai Chi Wo (22°32'01.5"N 114°16'04.1"E), respectively, during the summer and fall of 2017 (Fig. 1). We collected the coral samples during June to September 2017 when the three species were found to undergo bleaching, tagged bleached colonies and revisited them roughly three months later (Ip et al., 2022; Zhang et al., 2022). The seawater surface temperature recorded from sites near these coral communities ranged from 26.2 °C to 31.4 °C when bleaching was found (details in Supplementary Fig. S1). We used the Coral Health Chart of CoralWatch (Siebeck et al., 2006) to help determine the bleached and non-stressed colonies during the field sampling. There were four health conditions: (1) 'unbleached': a fragment from a colony without bleaching; (2) 'stressed-unbleached': an unbleached fragment from a partially bleached colony; (3) 'stressed-bleached': a bleached fragment from the same colony as in the 'stressed-unbleached' condition; (4) 'recovered': a fragment from a colony recovered from partial bleaching. For each health condition, we collected four biological replicates (colonies) at least two meters apart to avoid sampling of clones. Samples were kept in

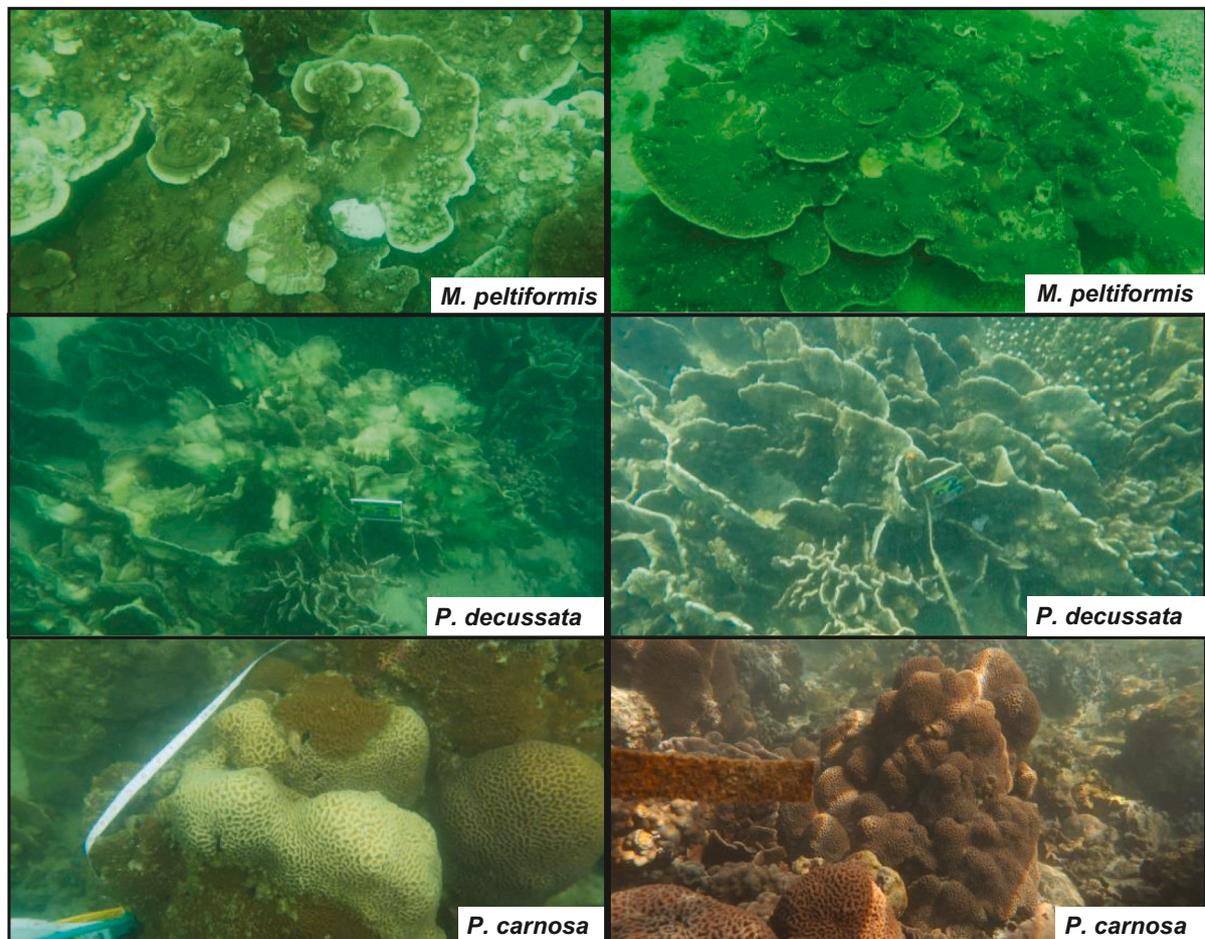


Fig. 1. Photographs of *Montipora peltiformis* (sampling site: Bluff Island), *Pavona decussata* (Sharp Island), and *Platygyra carnosa* (Lai Chi Wo) show the paled/bleached (left) and recovered (right) colonies during and after the 2017 bleaching event.

dry ice until being placed in the -80°C freezer within four hours.

Coral samples were grounded in liquid nitrogen with a mortar and pestle, and genomic DNA was extracted using the CTAB method (Por-
 ebski et al., 1997). We qualified and quantified DNA using agarose gel
 electrophoresis and a Qubit fluorometer (Thermo Fisher Scientific,
 USA), respectively. We submitted DNA samples to Novogene (Tianjin,
 China) for high-throughput sequencing of the internal transcribed
 spacer 2 (ITS2) region using the dinoflagellate-specific primers ITSInt-
 For2 (5'-GAATTGCAGAACTCCGTG -3' (LaJeunesse and Trench, 2000)
 and ITS-Reverse (5'-GGGATCCATATGCTTAAGTTCAGCGGGT -3'
 (Coleman et al., 2010). The sequencing libraries were prepared using the
 NEBNext Ultra DNA Library Prep Kit (Illumina, USA) and sequenced on
 an Illumina NovaSeq sequencer to obtain paired-end reads with a read
 length of 250 bp. There were four amplicon libraries for *M. peltiformis*,
 but only three amplicon libraries for *P. decussata* and *P. carnosa* due to
 the small amount of genomic DNA available for these two species.

The SymPortal framework v0.3.22 was used locally to analyze the
 Symbiodiniaceae ITS2 data (Hume et al., 2019). Briefly, we quality
 filtered all demultiplexed and paired forward and reverse fastq.gz files
 using mothur v1.43.0 (Schloss et al., 2009), conducted BLASTn search
 for Symbiodiniaceae sequences (184–310 bp), and then collapsed the
 variants using minimum entropy decomposition (Eren et al., 2015).
 After quality control, we predicted the ITS2-type profiles (the taxonomic
 unit of SymPortal) and characterized them through identification of co-
 occurring defining intragenomic variants (DIVs) within samples, and
 those in the existing database. Principal coordinate analyses (PCoA)
 were conducted based on the Bray–Curtis distance matrices obtained
 from the SymPortal as part of the output files. We tested significant
 differences among host species and health conditions with Permutational
 Multivariate Analysis of Variance (PERMANOVA) using the
 “adonis2” function in the R package “vegan”. We used a one-way

Analysis of Variance (ANOVA) followed by the Tukey test to compare
 each ITS2-type with relative abundance $>1\%$ among the four health
 conditions using SPSS Statistics 19 (SPSS Inc., Illinois, USA).

ITS2 amplicon sequencing ($n = 40$) generated a total of 3.59 million
 pair-end reads (average = 9.0 thousand reads per sample) from three
 coral species (Supplementary Table S1). Among these reads, SymPortal
 revealed 7,753 Symbiodiniaceae ITS2 sequence variants (DIVs) and
 further clustered them into 62 endosymbiotic ITS2-types belonging to
 the genus *Cladocopium* (formerly Clade C; Fig. 2; details in Supplemen-
 tary Table S2). Of the 62 endosymbiont ITS2-types, 45 (72 %) were not
 characterized by SymPortal, therefore were considered as novel types.
 To characterize these novel genotypes, we conducted BLASTn search
 against the SymPortal reference ITS2 database, which revealed a total of
 20 C1 variants, 11 C3 variants, 22 C21 variants, and 9 other genotypes of
Cladocopium according to Symbiodiniaceae phylogenetic relationships
 (Supplementary Table S2, LaJeunesse, 2005; LaJeunesse et al., 2018). In
 addition, in all collection times, SymPortal revealed *Cladocopium* 1466-
 C21-C1-4118-C3 as the single ITS2-type profile in all *M. peltiformis*
 samples, and *Cladocopium* C1-C1c-1466 as the only profile for all
P. decussata and *P. carnosa* samples (Fig. 1).

To understand the general endosymbiont composition within each
 species, we examined the ITS2-type and -abundance at species-level,
 combining all coral samples collected during and after the bleaching
 event. Samples of *M. peltiformis* (Supplementary Table S2) harbored 20
 to 25 ITS2-types; among them three C21 variants (average 42.9 % of
 1466_C, 18.4 % of C21, and 4.9 % of 4118_C), C1 (7.0 %), and C3 (3.9 %)
 were predominant, accounting for 80 % of the total abundance. All other
M. peltiformis genotypes were of low abundances (1.0–2.4 %), including
 two C3 variants (C3.14 and 5864_C) and six C21 variants (C21ac, C21k,
 5865_C, 5866_C, 5867_C, and 5869_C). Samples of *P. decussata* were
 associated with 16 to 24 ITS2-types, with C1 (59.9 %), C1c (17.4 %), and

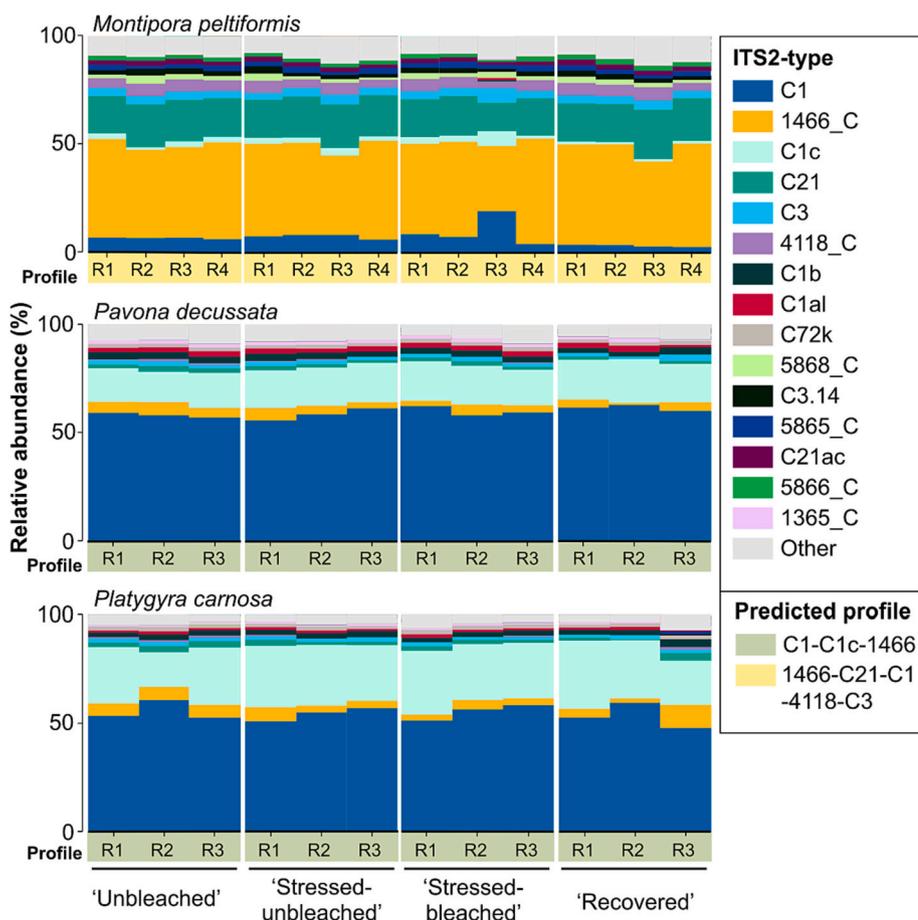


Fig. 2. Symbiodiniaceae community composition of three coral species during and after the 2017 bleaching event. Relative abundance (%) of ITS2-types from four health conditions is plotted above the horizontal black line (in X-axis). The predicted ITS2-type profile is plotted below. Only the top 15 relative abundance ITS2-types are shown, other sequences are represented by grey bars on the top. Designated names (e.g., C1) represent ITS2 sequences characterized in the SymPortal (Hume et al., 2019), while the uncharacterized/novel sequences are designated to a unique ID with the associated clade/genera (e.g., 1466_C). Sampling sites: Bluff Island (*Montipora peltiformis*), Sharp Island (*Pavona decussata*), and Lai Chi Wo (*Platygyra carnosa*).

1466_C (4.0 %) being most dominant; all samples contained five low abundance *Cladocopium*, including C1b, C1a1, C3, C72k, and 1365_C. Samples of *P. carnososa* exhibited similar endosymbiont composition with *a. decussata*, consisting of C1 (54.9 %), C1c (25.8 %), and 1466_C (4.9 %) and five low abundance ITS2-types (C1b, C3, C21, C72k, and 1373_C) in all samples. Notably, we also detected 20, 9, and 7 unique ITS2-types in *M. peltiformis*, *P. decussata*, and *P. carnososa*, respectively (Supplementary Fig. S2). These genotypes were closely related to lineages of C21 in *M. peltiformis* and C1 in *P. decussata* and *P. carnososa*, respectively.

To reveal the potential changes in symbiont composition during the bleaching event, we compared the endosymbiont community structure among coral species and health conditions. The endosymbiont community structure exhibited a high level of host-specificity (PERMANOVA, $F = 520.38$, $R^2 = 0.965$, $p < 0.0001$; Supplementary Table S3), while the PCoA plot revealed clustering of samples by species (Fig. 3), further confirming host identity as the major contributor for the differences in endosymbiont community structure among the samples. Each coral host was associated with three to five predominant endosymbionts that were present in the three coral species in different proportions. Notably, four ITS2-types (C1, C1c, C21, and 1466_C) were among the most abundant endosymbiotic dinoflagellates (Supplementary Fig. S2) in the three coral species under all four health conditions.

Within each species, the endosymbiont types generally did not vary significantly among the four health conditions (PERMANOVA, $F = 1.52$, $R^2 = 0.004$, $p = 0.226$). Nevertheless, when we compared each ITS2-type (relative abundance $> 1\%$) among the four health conditions within each coral host, we found that the 'recovered' *M. peltiformis* samples contained lower proportions of C1 (3.4 %) and C1c (1.1 %) than the other health conditions (6.9 %–10.0 % and 2.3 %–3.5 %, respectively; Tukey test, $p > 0.05$; Supplementary Table S4). Although there was a reducing tendency of C21 types in 'stressed-bleached' *M. peltiformis*

(71.5 %), compared with the other health conditions (75.3 %–80.4 %), this difference was not statistically significant. In addition, there was a slight increase in C1c in the stressed *P. decussata* (17.6 %–18.8 %), compared with the 'unbleached' corals (15.2 %), although the differences were insignificant. In *P. carnososa*, there was no significant difference among the four health conditions, except for a slightly lower abundance of C1c in the 'unbleached' condition (22.8 %) than in other conditions (26.2 %–27.2 %). Thus, our results showed that the coral host was the primary determining factor of endosymbiont variability. Among the three coral species, 'stressed-bleached' *M. peltiformis* (32) was associated with more ITS2-types than the other two species (26 in *P. decussata* and 19 in *P. carnososa*; Supplementary Fig. S2), and there were slight changes in C1 and C1c, which are two ITS2 genotypes common to the subtropical corals of Hong Kong, Guangdong Province, and Guangxi Province in the South China Sea (Chen et al., 2019; Saad et al., 2021).

In each coral species, we observed a high host fidelity in their predominant endosymbiotic dinoflagellates: *Cladocopium* C21 in *M. peltiformis*, and C1/C1c in *P. decussata* and *P. carnososa*. These ITS2 types have been reported in non-bleached corals in Hong Kong previously (Tong et al., 2017; Saad et al., 2021). The dominance of *Cladocopium* has also been reported in nearby subtropical coral communities in Taiwan (Chen et al., 2005) and the South China Sea (Gong et al., 2018; Chen et al., 2019). Such host specificity within a region has been reported in tropical and subtropical coral reefs [e.g., Australia's Great Barrier Reef (Tonk et al., 2013), the Red Sea (Hume et al., 2020; Osman et al., 2020), the Andaman Sea and Zanzibar (LaJeunesse et al., 2010)]. The host-symbiont fidelity in Hong Kong likely indicates strong local selection pressure to the subtropical climate (Saad et al., 2021). A similar high fidelity of host-symbiont association after bleaching was reported for corals inhabiting the northern Red Sea (Hume et al., 2020; Woolstra et al., 2021), and this has been suggested as a specific adaptation to the relatively warm water that has selected the heat-resistant Symbiodiniaceae (Silverstein et al., 2015; Boulotte et al., 2016). In corals of the Persian/Arabian Gulf, Smith et al. (2017) reported stability of endosymbiont composition, with *Cladocopium* C3 being the dominant genotype in the lagoonal reefs, and no increase in the proportion of *Durussidinium* during and after a bleaching event. They proposed that this was due to the absence of a more heat tolerant genotype than the dominant C3 in the study region. Notably, our SymPortal analysis revealed 45 out of 64 ITS2-types as novel *Cladocopium* types. Our BLASTn search revealed that 59 of them were highly homologous with the Symbiodiniaceae types that have previously been reported in the South China Sea (Chen et al., 2019), with sequence identities of 99.2 % to 100 % (Supplementary Table S5). Importantly, the presence of 22 C1 and 19 C21 variants might imply the genetic divergence of symbionts, and the proliferation of these Symbiodiniaceae genotypes has been suggested to be the result of niche diversification unique to the subtropical climate of Hong Kong (Ng and Ang, 2016; Wong et al., 2016; Saad et al., 2021).

Our previous field and laboratory studies revealed differential sensitivity to heatwave in the three coral species, with *P. decussata* and *P. carnososa* being most resilience than *M. peltiformis* (Xie et al., 2020; Ip et al., 2022; Zhang et al., 2022). Specifically, the bleaching susceptible *M. peltiformis* was associated with host-specialist symbiont *Cladocopium* C21 with relative higher symbiont diversity, which is restricted to only a few exposed sites facing the open ocean. The resilient *P. decussata* and *P. carnososa* were associated with host-generalist C1 with lower symbiont diversity, and they are widely distributed in the protected bays of eastern Hong Kong waters (Yeung et al., 2021). These results appeared to lend support to the speculation that the low symbiont diversity is an adaptive mechanism in marginal coral communities, where the strong selective pressure may favor the selection of certain well-adapted genotypes (Ng and Ang, 2016; Smith et al., 2020; Saad et al., 2021). Therefore, corals hosting generalist C1/C1c possibly exhibit higher stress resilience than those associated with specialist C21.

Although Hong Kong's coral communities have suffered from three

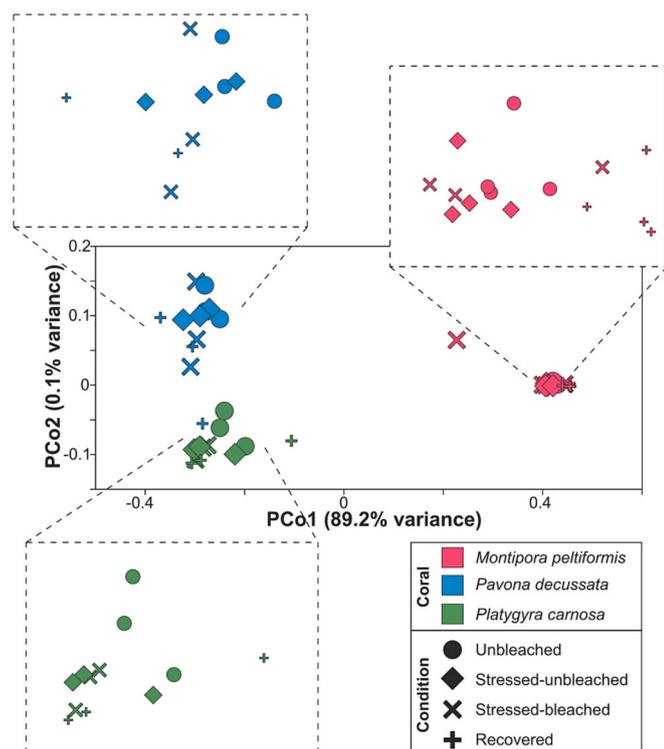


Fig. 3. Principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity matrix of Symbiodiniaceae communities associated with three coral species and four health conditions during and after the 2017 bleaching event. PCoA shows the clustering pattern between coral species. The dashed box shows the zoomed-in view of each species. Sampling sites: Bluff Island (*Montipora peltiformis*), Sharp Island (*Pavona decussata*), and Lai Chi Wo (*Platygyra carnososa*).

bleaching events, i.e., 1997–1998, 2014, and 2017, little is known about the endosymbionts' responses in these marginal corals. Here, for the first time, we provided compositional details of the endosymbiotic dinoflagellates in three coral species in the subtropical Hong Kong waters during and after the 2017 bleaching event. We showed that endosymbiont community composition might have contributed to the differential bleaching susceptibility of the three coral species. Specifically, *P. carcosa* and *P. decussata* with a high proportion of generalist C1/C1c types had better resilience to heatwave as evidenced by lower reductions in algal symbiont and coral pigmentation (Ip et al., 2022; Zhang et al., 2022). The more susceptible *M. peltiformis* having a larger loss of endosymbiont density and stronger photoinhibition in the remaining endosymbiont (Ip et al., 2022) hosted the specialist C21 types. In addition, we identified 45 novel *Cladocopium* types, highlighting the genetic diversity of endosymbionts inhabiting the northern South China Sea. Overall, our study has provided new knowledge on the changes in coral Symbiodiniaceae composition during a subtropical bleaching event, and a baseline for future coral research and management in Hong Kong and the surrounding Greater Bay Area. The results highlight the importance of locally adapted genotypes in coral reef resilience.

CRedit authorship contribution statement

JWQ designed the research. YHY and JYX collected the samples. YZ extracted the DNA. JCHI analyzed the data and drafted the manuscript. All authors edited the manuscript and approved the submission.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Sequence data determined in this study are available in the NCBI SRA database under the BioProject PRJNA884862.

Acknowledgments

Funding for this project was provided by the Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou) (GML2019ZD0404, GML2019ZD0409, and L2019005), General Research Fund of Hong Kong (12102018), and Hong Kong Baptist University's Start-up Grant for New Academics (162780).

Appendix A. Supplementary Figures S1-S2 and Supplementary Tables S1-S5

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2022.114224>.

References

Alemu, J.B., Clement, Y., 2014. Mass coral bleaching in 2010 in the southern Caribbean. *PLoS One* 9, e83829.

Baker, A.C., 2003. Flexibility and specificity in coral-alga symbiosis: diversity, ecology and biogeography of symbiodinium. *Annu. Rev. Ecol. Evol. Syst.* 34, 661–689.

Beger, M., Sommer, B., Harrison, P.L., Smith, S.D., Pandolfi, J.M., 2014. Conserving potential coral reef refuges at high latitudes. *Divers. Distrib.* 20, 245–257.

Boulotte, N.M., Dalton, S.J., Carroll, A.G., Harrison, P.L., Putnam, H.M., Peplow, L.M., van Oppen, M.J.H., 2016. Exploring the Symbiodinium rare biosphere provides evidence for symbiont switching in reef-building corals. *ISME J.* 10, 2693–2701.

Chan, A.L.K., Chan, K.K., Choi, C.L.S., McCorry, D., Lee, M.W., Ang, P., 2005. Field Guide to Hard Corals of Hong Kong. Agriculture, Fisheries and Conservation Department, The Hong Kong SAR Government.

Chen, C.A., Yang, Y.W., Wei, N.V., Tsai, W.S., Fang, L.S., 2005. Symbiont diversity in scleractinian corals from tropical reefs and subtropical non-reef communities in Taiwan. *Coral Reefs* 24, 11–22.

Chen, B., Yu, K., Liang, J., Huang, W., Wang, G., Su, H., Qin, Z., Huang, X., Pan, Z., Luo, W., 2019. Latitudinal variation in the molecular diversity and community composition of symbiodiniaceae in coral from the South China Sea. *Front. Microbiol.* 10, 1278.

Claar, D.C., Starko, S., Tietjen, K.L., Epstein, H.E., Cuning, R., Cobb, K.M., Baker, A.C., Gates, R.D., Baum, J.K., 2020. Dynamic symbioses reveal pathways to coral survival through prolonged heatwaves. *Nat. Commun.* 11, 1–10.

Coleman, A.W., Arturo, S., Goff, L.J., 2010. Molecular delineation of species and syngens in volvocacean green algae (Chlorophyta). *J. Phycol.* 30, 80–90.

Eakin, C.M., Sweatman, H.P., Brainard, R.E., 2019. The 2014–2017 global-scale coral bleaching event: insights and impacts. *Coral Reefs* 38, 539–545.

Eddy, T.D., Lam, V.W., Reygondeau, G., Cisneros-Montemayor, A.M., Greer, K., Palomares, M.L.D., Bruno, J.F., Ota, Y., Cheung, W.W., 2021. Global decline in capacity of coral reefs to provide ecosystem services. *One Earth* 4, 1278–1285.

Eren, A.M., Morrison, H.G., Lescault, P.J., Reveillaud, J., Vineis, J.H., Sogin, M.L., 2015. Minimum entropy decomposition: unsupervised oligotyping for sensitive partitioning of high-throughput marker gene sequences. *ISME J.* 9, 968–979.

Fuller, Z.L., Mocellin, V.J., Morris, L.A., Cantin, N., Shepherd, J., Sarre, L., Peng, J., Liao, Y., Pickrell, J., Andolfatto, P., 2020. Population genetics of the coral *Acropora millepora*: toward genomic prediction of bleaching. *Science* 369, eaba4674.

Gardner, S.G., Camp, E.F., Smith, D.J., Kahlke, T., Osman, E.O., Gendron, G., Hume, B.C., Pogoreutz, C., Voolstra, C.R., Suggett, D.J., 2019. Coral microbiome diversity reflects mass coral bleaching susceptibility during the 2016 El Niño heat wave. *Ecol. Evol.* 9, 938–956.

Glynn, P.W., 1991. Coral reef bleaching in the 1980s and possible connections with global warming. *Trends Ecol. Evol.* 6, 175–179.

Gong, S., Chai, G., Xiao, Y., Xu, L., Yu, K., Li, J., Liu, F., Cheng, H., Zhang, F., Liao, B., 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.

Goreau, T., McClanahan, T., Hayes, R., Strong, A., 2000. Conservation of coral reefs after the 1998 global bleaching event. *Conserv. Biol.* 14, 5–15.

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

Hume, B.C.C., Voolstra, C.R., Arif, C., D'Angelo, C., Burt, J.A., Eyal, G., Loya, L., Wiedenmann, J., 2016. Ancestral genetic diversity associated with the rapid spread of stress-tolerant coral symbionts in response to Holocene climate change. *Proc. Natl. Acad. Sci. U. S. A.* 113, 4416–4421.

Hume, B.C., Smith, E.G., Ziegler, M., Warrington, H.J., Burt, J.A., LaJeunesse, T.C., Wiedenmann, J., Voolstra, C.R., 2019. SymPortal: a novel analytical framework and platform for coral algal symbiont next-generation sequencing ITS2 profiling. *Mol. Ecol. Resour.* 19, 1063–1080.

Hume, B.C., Mejia-Restrepo, A., Voolstra, C.R., Berumen, M.L., 2020. Fine-scale delineation of Symbiodiniaceae genotypes on a previously bleached central Red Sea reef system demonstrates a prevalence of coral host-specific associations. *Coral Reefs* 39, 583–601.

Ip, J.C.H., Zhang, Y., Xie, J.Y., Yeung, Y.H., Qiu, J.W., 2022. Comparative transcriptomics of two coral holobionts collected during the 2017 El Niño heat wave reveal differential stress response mechanisms. *Mar. Pollut. Bull.* 182, 114017.

IPCC, 2014. In: *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland, p. 151.

LaJeunesse, T.C., 2005. "Species" radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. *Mol. Biol. Evol.* 22, 570–581.

LaJeunesse, T.C., Trench, R.K., 2000. Biogeography of two species of symbiodinium (Freudenthal) inhabiting the intertidal sea anemone *Anthopleura elegantissima* (Brandt). *Biol. Bull. U.S.* 199, 126–134.

LaJeunesse, T.C., Bhagooli, R., Hidaka, M., deVantier, L., Done, T., Schmidt, G.W., Fitt, W.K., Hoegh-Guldberg, O., 2004. Closely related symbiodinium spp. Differs in relative dominance in coral reef host communities across environmental, latitudinal and biogeographic gradients. *Mar. Ecol. Prog. Ser.* 284, 147–161.

LaJeunesse, T.C., Pettay, D.T., Sampayo, E.M., Phongsuwan, N., Brown, B., Obura, D.O., Hoegh-Guldberg, O., Fitt, W.K., 2010. Long-standing environmental conditions, geographic isolation and host-symbiont specificity influence the relative ecological dominance and genetic diversification of coral endosymbionts in the genus symbiodinium. *J. Biogeogr.* 37, 785–800.

LaJeunesse, T.C., Parkinson, J.E., Gabrielson, P.W., Jeong, H.J., Reimer, J.D., Voolstra, C.R., Santos, S.R., 2018. Systematic revision of symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. *Curr. Biol.* 28, 2570–2580.

McCorry, D., 2002. Hong Kong's Scleractinian Coral Communities: Status, Threats and Proposals for Management. PhD Thesis. The University of Hong Kong, Hong Kong.

Morton, B., Morton, J., 1983. *The Sea Shore Ecology of Hong Kong*. Hong Kong University Press, Hong Kong.

Mostafavi, P.G., Fatemi, S.M.R., Shahhosseini, M.H., Hoegh-Guldberg, O., Loh, W.K.W., 2007. Predominance of clade D symbiodinium in shallow water reef-building corals off Kish and Larak Islands (Persian gulf, Iran). *Mar. Biol.* 153, 25–34.

Ng, T.Y., Ang, P., 2016. Low symbiont diversity as a potential adaptive strategy in a marginal non-reef environment: a case study of corals in Hong Kong. *Coral Reefs* 35, 941–957.

Osman, E.O., Suggett, D.J., Voolstra, C.R., Pettay, D.T., Clark, D.R., Pogoreutz, C., Sampayo, E.M., Warner, M.E., Smith, D.J., 2020. Coral microbiome composition along the northern Red Sea suggests high plasticity of bacterial and specificity of endosymbiotic dinoflagellate communities. *Microbiome* 8, 1–16.

Pochon, X., Gates, R.D., 2010. A new symbiodinium clade (Dinophyceae) from soritid foraminifera in Hawai'i. *Mol. Phylogenet. Evol.* 56, 492–497.

- Porebski, S., Bailey, L.G., Baum, B.R., 1997. Modification of a CTAB DNA extraction protocol for plants containing high polysaccharide and polyphenol components. *Plant Mol. Biol. Rep.* 15, 8–15.
- Russnak, V., Rodriguez-Lanetty, M., Karsten, U., 2021. Photophysiological tolerance and thermal plasticity of genetically different symbiodiniaceae endosymbiont species of cnidaria. *Front. Mar. Sci.* 8, 657348.
- Saad, O.S., Lin, X., Ng, T.Y., Li, L., Ang, P., Lin, S., 2021. Species richness and generalists–specialists mosaicism of symbiodiniacean symbionts in corals from Hong Kong revealed by high-throughput ITS sequencing. *Coral Reefs* 41, 1–12.
- Schloss, P.D., Westcott, S.L., Ryabin, T., Hall, J.R., Hartmann, M., Hollister, E.B., Lesniewski, R.A., Oakley, B.B., Parks, D.H., Robinson, C.J., Sahl, J.W., Stres, B., Thallinger, G.G., Van Horn, D.J., Weber, C.F., 2009. Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Appl. Environ. Microbiol.* 75, 7537–7541.
- Siebeck, U.E., Marshall, N.J., Klüter, A., Hoegh-Guldberg, O., 2006. Monitoring coral bleaching using a colour reference card. *Coral Reefs* 25, 453–460.
- Silverstein, R.N., Cuning, R., Baker, A.C., 2015. Change in algal symbiont communities after bleaching, not prior heat exposure, increases heat tolerance of reef corals. *Glob. Chang. Biol.* 21, 236–249.
- Smith, E., Vaughan, G., Ketchum, R., McParland, D., Burt, J., 2017. Symbiont community stability through severe coral bleaching in a thermally extreme lagoon. *Sci. Rep.* 7, 1–9.
- Smith, E.G., Gurskaya, A., Hume, B.C., Voolstra, C.R., Todd, P.A., Bauman, A.G., Burt, J. A., 2020. Low symbiodiniaceae diversity in a turbid marginal reef environment. *Coral Reefs* 39, 545–553.
- Sully, S., Burkepille, D.E., Donovan, M., Hodgson, G., Van Woesik, R., 2019. A global analysis of coral bleaching over the past two decades. *Nat. Commun.* 10, 1–5.
- Tong, H., Cai, L., Zhou, G., Yuan, T., Zhang, W., Tian, R., Huang, H., Qian, P.Y., 2017. Temperature shapes coral-algal symbiosis in the South China Sea. *Sci. Rep.* 7, 1–12.
- Tonk, L., Sampayo, E.M.E., Weeks, S.S.S., Magno-Canto, M., Hoegh-Guldberg, O., Hoegh-Guldberg, O., 2013. Host-specific interactions with environmental factors shape the distribution of symbiodinium across the great barrier reef. *PLoS One* 8, e68533.
- Voolstra, C.R., Valenzuela, J.J., Turkarslan, S., Cárdenas, A., Hume, B.C., Perna, G., Buitrago-López, C., Rowe, K., Orellana, M.V., Baliga, N.S., 2021. Contrasting heat stress response patterns of coral holobionts across the Red Sea suggest distinct mechanisms of thermal tolerance. *Mol. Ecol.* 30, 4466–4480.
- Wilkinson, C.C., 1998. The 1997–1998 mass bleaching event around the world. In: Wilkinson, C. (Ed.), *Status of Coral Reefs of the World: 2000*. Australian Institute of Marine Science, Townsville, pp. 15–38.
- Wong, J.C., Thompson, P., Xie, J.Y., Qiu, J.W., Baker, D.M., 2016. Symbiodinium clade C generality among common scleractinian corals in subtropical Hong Kong. *Reg. Stud. Mar. Sci.* 8, 439–444.
- Xie, J.Y., Lau, D.C., Kei, K., Vriko, P., Chow, W.K., Qiu, J.W., 2017. The 2014 summer coral bleaching event in subtropical Hong Kong. *Mar. Pollut. Bull.* 124, 653–659.
- Xie, J.Y., Yeung, Y.H., Kwok, C.K., Kei, K., Ang, P., Chan, L.L., Cheang, C.C., Chow, W.K., Qiu, J.W., 2020. Localized bleaching and quick recovery in Hong Kong's coral communities. *Mar. Pollut. Bull.* 153, 110950.
- Yeung, Y.H., Xie, J.Y., Kwok, C.K., Kei, K., Ang, P., Chan, L.L., Dellisanti, W., Cheang, C. C., Chow, W.K., Qiu, J.W., 2021. Hong Kong's subtropical scleractinian coral communities: baseline, environmental drivers and management implications. *Mar. Pollut. Bull.* 167, 112289.
- Yorifuji, M., Yamashita, H., Suzuki, G., Kawasaki, T., Tsukamoto, T., Okada, W., Tamura, K., Nakamura, R., Inoue, M., Yamazaki, M., 2021. Unique environmental symbiodiniaceae diversity at an isolated island in the northwestern Pacific. *Mol. Phylogenet. Evol.* 161, 107158.
- Zhang, Y., Ip, J.C.H., Xie, J.Y., Yeung, Y.H., Sun, Y., Qiu, J.W., 2022. Host–symbiont transcriptomic changes during natural bleaching and recovery in the leaf coral *Pavona decussata*. *Sci. Total Environ.* 806, 150656.
- Zhao, Y., Law, Y.S., Zhai, X., Zhou, K., Chen, M., Qiu, J.W., 2022. Urban coral communities and water quality parameters along the coasts of Guangdong Province, China. *Mar. Pollut. Bull.* 180, 113821.
- Ziegler, M., Arif, C., Burt, J.A., Dobretsov, S., Order, C., LaJeunesse, T.C., Voolstra, C.R., 2017. Biogeography and molecular diversity of coral symbionts in the genus symbiodinium around the arabian peninsula. *J. Biogeogr.* 44, 674–686.