



Differential Symbiodiniaceae Association With Coral and Coral-Eroding Sponge in a Bleaching Impacted Marginal Coral Reef Environment

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Marginal reefs are known for severe stress-inducible perturbations such as high sedimentation, eutrophication, ocean warming, and acidification from anthropogenic climate change. The corals striving in such stressful environments develop physiological adaptations induced by differential genomic expressions or association with thermal stress-tolerant algal symbionts (Symbiodiniaceae). Despite such adaptations, corals are threatened by other space competitors such as algae and sponges. Coral-eroding sponges belonging to the *Cliona viridis* complex are one such space competitors that also associate with Symbiodiniaceae algal photosymbiont. The diversity of Symbiodiniaceae associates with the coral and sponge from the same ecosystems is scarcely known. In the present study, Symbiodiniaceae community structure in the coral *Turbinaria mesenterina*, a newly described coral-eroding sponge *Cliona thomasi*, and their surrounding seawater was determined from the nearshore marginal reef along the central west coast of India. The results revealed a significantly higher relative abundance of *Durusdinium* and *Gerakladium* than *Symbiodinium* and *Cladocopium* in the seawater. Interestingly, both investigated host species showed differential Symbiodiniaceae association with significantly higher abundance of *Durusdinium* in coral and *Gerakladium* in sponge. The beta diversity analysis by Permutational multivariate analysis of variance (PERMANOVA) confirmed significant differences in Symbiodiniaceae profiles between sponge and coral. *Durusdinium* and *Gerakladium* are thermotolerant genera known to associate with different hosts in suboptimal conditions. Our field surveys suggested the bleaching resistance of the coral *T. mesenterina* despite the fact that the sea surface temperature reached the coral thermal threshold of 31°C during different periods of the years 2015, 2016, 2017, 2018, and 2019. Therefore, the thermal tolerance of the investigated coral and sponge species may be attributed to their respective thermotolerant photosymbiont associations. Furthermore, the results also indicated the host-specific

photosymbiont selection from the local environment. Although these observations provide valuable biological insight, more research is needed to understand the tripartite association of sponge-coral-symbiont together to evaluate the competitive fitness of holobionts.

Keywords: coral, sponge, *Cliona*, *Turbinaria*, Symbiodiniaceae, symbiont, ITS2, bioerosion

INTRODUCTION

Coral reefs harbor the most dynamic and complex plethora of microbial communities, including bacteria, fungi, viruses, archaea, and dinoflagellates (Mies et al., 2017; Osman et al., 2020; Pernice et al., 2020). Endosymbiotic dinoflagellates of the Symbiodiniaceae family have gained considerable attention as an indicator for the well-being of the coral reef health and ecosystem functioning (Silverstein et al., 2012; Osman et al., 2020). Symbiodiniaceae are present in the coral's ambient environment (seawater and sediment) as free-living form as well as in association with different host organisms like sponges, foraminifera, clams, etc. (Takabayashi et al., 2012; Granados-Cifuentes et al., 2015). Free-living Symbiodiniaceae are crucial pool of photosymbiont for host organisms, as they acquired new symbiont from the ambient environment at different life stages (Granados-Cifuentes et al., 2015; Nitschke et al., 2016). Endosymbionts of reef-building corals contribute to most of the energy requirement of coral through photosynthesis, enabling calcium carbonate accretion and growth (Al-Horani, 2016). In return, coral supports Symbiodiniaceae by providing a protective environment and necessary components required for photosynthesis (Williams and Patterson, 2020). The dynamics in coral-Symbiodiniaceae interaction influences the ability of corals to function under different environmental conditions (Jones et al., 2008; Ziegler et al., 2017). The association of coral with different Symbiodiniaceae is regulated by local environmental conditions (Thornhill et al., 2017; Baker et al., 2018). So far, obligatory symbiosis of corals with different Symbiodiniaceae genera has been documented from a broad geographical and environmental regimes, that include *Symbiodinium*, *Breviolum*, *Cladocopium*, *Durusdinium* and, occasionally *Fugacium* and *Gerakladium* (formerly clades A, B, C, D, F, and G, respectively) (LaJeunesse et al., 2018; Osman et al., 2020). Each symbiont genus provides a different degree of support to the host coral (Stat et al., 2008; Camp et al., 2020; Pernice et al., 2020). For instance, Symbiodiniaceae diversity in *Leptoria phrygia*, experiencing thermal instability showed an exclusive association with *Durusdinium* for coping with thermal stress (Carballo-Bolaños et al., 2019). Furthermore, D'Angelo et al. (2015) confirmed the specific association of different *Porites* spp. with *Cladocopium* (C3) type symbiont in the warm and hypersaline waters of the Persian/Arabian Gulf.

Recent studies have confirmed that some corals (e.g., *Montastraea cavernosa*, *Pocillopora damicornis*, *Stylophora pistillata*, and *Porites lutea*) can adapt, sustain, and survive against local environmental stressors by switching or shuffling their associated photosymbionts (Silverstein et al., 2015; Boulotte et al., 2016; Osman et al., 2018; Tan et al., 2020). Response

to environmental stressors varies among coral species and endosymbiont communities (van Woesik et al., 2011; Cunning et al., 2017). The local environment exerts selection pressure which eliminates the sensitive Symbiodiniaceae taxa and results in the dominance of stress-resilient species (Cunning et al., 2015; Claar et al., 2020). This differential abundance of specific thermotolerant Symbiodiniaceae taxa affects the functional characteristics of their host (LaJeunesse et al., 2010a; Carballo-Bolaños et al., 2019), eventually leading to the emergence of a particular "space winner" genotype (LaJeunesse et al., 2010a; Stat and Gates, 2011).

Globally, coral reefs are under threat due to climate change induced thermal stress and anthropogenic impacts, which disrupt delicate coral-Symbiodiniaceae interaction, causing mass coral bleaching, mortality, and rapid health deterioration of reef ecosystems (Hughes et al., 2017, 2018). Moreover, increasing disturbance may contribute to the overgrowth of benthic space competitors like cyanobacterial mats, macroalgae, and sponges, which pose additional threats to stressed reef-building corals (Horwitz et al., 2017). Among these benthic space competitors, bioeroding sponges are one of the most aggressive competitors that are known to erode reef-building corals and destruct the reef (Schönberg, 2000; Zundeleich et al., 2007; Fang et al., 2018b). For instance, species belonging to *Cliona viridis* species complex accounts for significant erosion of corals at the rate of >10 kg/m sponge area/year (Schönberg, 2000; Achlatis et al., 2019). The cosmopolitan sponge genus *Cliona* consists of 86 species (Van Soest et al., 2020), and among those, only about 25% of species are known to harbor symbiotic dinoflagellate communities (Achlatis, 2018; Mote et al., 2019). Studies have shown that algal symbionts of *Cliona* species provide their host with energetic inputs needed for excavating calcium carbonate through investment in photosynthates and/or photosynthesis by-products (Marlow et al., 2018; Achlatis et al., 2019). These symbionts occur in high densities in *Cliona viridis* species complex and display remarkably rapid lateral expansion and high bioerosion rates (Schönberg et al., 2008; Hill et al., 2011). Therefore, Symbiodiniaceae family members support their bioeroding host in space competition as well as in coping with the fluctuating environmental conditions (Fang et al., 2017, 2018b).

A few studies have shown that some sponges are associated with algal symbionts from *Symbiodinium*, *Breviolum*, and *Gerakladium* genera (formerly clades A, B, and G) (Hill et al., 2011; Ramsby et al., 2017). Moreover, these Symbiodiniaceae diversity analyses were mainly based on specific and/or multiple gene amplification followed by sequencing (Hill et al., 2011; Ramsby et al., 2017). However, the application of the next-generation sequencing (NGS) approach to dissect the taxonomic

diversity of Symbiodiniaceae family associated with sponges is sparsely studied compared with other invertebrates (Riesgo et al., 2014; Ramsby et al., 2018). In order to gain insights into the role of Symbiodiniaceae members in the reef ecosystem, it is essential to study the multifaceted association between coral-symbiont, sponge-symbiont, and sponge-coral.

Determination of the composition and variability of symbiont community in reef-building corals and space-competing sponges is crucial to get an insight into how the symbiont compositional change influences the host's physiology and competitive abilities in response to suboptimal environmental conditions. Although previous studies significantly contributed to our understanding of coral-symbiont diversity and the environmental-induced plasticity, the understanding of symbiosis between bioeroding sponges and Symbiodiniaceae is still sparse. Therefore, the present study employed a deep sequencing approach to elucidate the Symbiodiniaceae diversity associated with the coral *Turbinaria mesenterina* and the bioeroding sponge *Cliona thomasi*, both competing in a marginal coral reef environment on the west coast of India. Shallow water nearshore coral reefs in this region are subjected to a broad range of chronic and acute stressors, which are considered suboptimal for coral reef development, including thermal stress-driven recurrent coral bleaching episodes (De et al., 2015, 2021; Hussain et al., 2016), coral diseases (Hussain et al., 2016), monsoonal freshwater influx, and anthropogenic perturbations like, siltation, turbidity, nutrient input, fishing, and intensive tourism-mediated damage (De et al., 2020). *C. thomasi* investigated herein is a newly discovered ecologically important sponge species, abundant in the Indian Ocean coral reefs (Mote et al., 2019). Therefore, aggressive growth of this species on live corals raises serious concern about reefs health (Mote et al., 2019).

MATERIALS AND METHODS

Study Site and Field Surveys

The study was conducted at the nearshore shallow water patch coral reef in the Grande Island archipelago, Central West Coast of India (15° 21' 14.2" N, 73° 45' 57.8" E). This nearshore patch coral reef on the Eastern Arabian Sea is highly disturbed by a wide range of stressors due to ongoing frequent thermal stress, low pH, monsoonal dilution of coastal seawater, higher sedimentation, and turbidity as two major rivers (Zuari and Mandovi rivers) discharge large amount of terrigenous sediment runoff and organic matter enrichment (Purnachandra Rao et al., 2011; Shynu et al., 2015; Veerasingam et al., 2015; Manikandan et al., 2016; Hussain and Ingole, 2020). The coral community in this reef habitat is mainly dominated by stress-resilient genera like *Porites*, *Siderastrea*, *Pseudosiderastrea*, *Coscinarea*, *Turbinaria*, and *Goniopora*; notably, sensitive branching taxa like *Acropora* are absent in this region (Hussain and Ingole, 2020). In recent years, corals in this nearshore habitat experienced an adverse impact from mass coral bleaching event (~50%) during 2014–2017 (Hussain and Ingole, 2020), along with overgrowth of coral-eroding *Cliona* sponges (Manikandan et al., 2016; Mote et al., 2019), algal turf, macroalgae (Manikandan et al., 2016),

coral diseases like white plaque and trematodiasis (Manikandan et al., 2016), and bioinvasion of alien octocoral *Carrijoa riisei* (Patro et al., 2015). The study area is under continuous monitoring for the coral reef health assessment program since 2015. The field surveys showed a massive bleaching of corals in 2015. These bleaching events were continuously observed under subsequent field surveys. Furthermore, an increase in the sponge prevalence was recorded during 2015–2017. The details of survey times, methodology applied to monitor and the prevalence of coral-eroding sponges, and coral bleaching from the study site are given in Supplementary Information.

Sample Collection

The samples of the bioeroding sponge *C. thomasi* ($n = 4$) growing over the coral (*T. mesenterina*) colonies and healthy coral species *T. mesenterina* ($n = 4$) were collected in January 2019 from the depth of 6–8 m. Massive growth forms of sponge species *C. thomasi* over different individual coral species are shown in **Figures 1a–d**. Utmost care was taken while collecting the samples, wherein each sample was distinct and separated from the other by at least 5 m. The coral and sponge tissue samples of ~1–2 cm² in diameter and 0.5–1 cm in thickness were collected using pre-cleaned hammers and chisels. To compare the community with the ambient environment, surrounding seawater samples ($n = 4$) were collected from a distance of 2–4 m away from sponge-coral colonies. Samples were immediately brought on board, fixed in liquid nitrogen, and transported to the laboratory for further processing. The sponge species was identified by spicule morphology and molecular analysis following the established protocol (Mote et al., 2019).

DNA Extraction and Sequencing

The total DNA from each collected sample was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. About 500 ml of seawater for each sample was filtered using 0.22 μm polycarbonate membrane filter (Whatman), and the filter paper was used for DNA isolation. For the identification of the Symbiodiniaceae community, the internal transcribed spacer 2 (ITS2) region was selected for amplification and sequencing using the primer set as forward 5'-GTGAATTGCAGAACTCCGTG-3' and reverse 5'-CCTCCGCTTACTTATATGCTT-3' (Boulotte et al., 2016). PCR amplifications were carried out in a 50-μl reaction volume containing ~50 ng of DNA, 25 μl of 2×Taq Platinum PCR Master, 200nM of each primer, and ddH₂O to make up the final volume. Reactions were performed at 95°C for 5 min, followed by 35 cycles of 95°C for 30 s, 51°C for 30 s, and 72°C for 30 s, and a final extension at 72°C for 4 min using a Mastercycler (Applied Biosystems, Foster City, United States). Illumina MiSeq libraries for the ITS2 region were generated and validated using 2100 Bioanalyzer (Agilent Technologies) for quality, and samples were sequenced using the 2 × 250 paired-end chemistry according to the manufacturer's specification (HiSeq Reagent Kit). Sequencing was done on the MiSeq Illumina platform and produced 4,525,076 paired-end raw reads with an average read length of ~350 to ~420 bp.

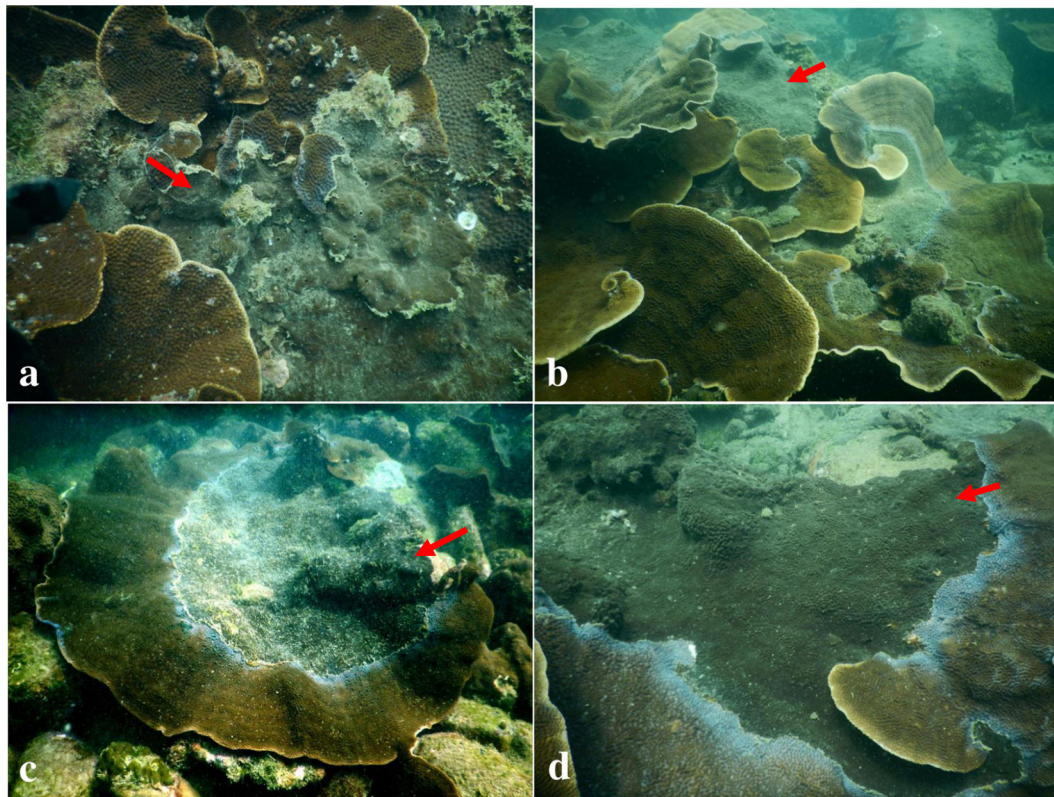


FIGURE 1 | Massive growth forms of *Cliona thomasi* observed over different live coral colonies of *Turbinaria mesenterina* (a–d) from the studied site Grande Island.

Bioinformatic Analysis

Sequence reads generated through the Illumina Miseq platform were demultiplexed, and primers were trimmed using Cutadapt (Martin, 2011). DADA2 pipeline recommended by Callahan et al. (2016) for ITS analysis based amplicon sequence variant (ASVs) generation was followed. The determined ITS2 ASVs were assigned a taxonomic identity using the RDP classifier (Wang et al., 2007) against reference database sequences. This study employed three different databases for taxonomic classification of ASVs: (i) Db1 (Claar et al., 2020), (ii) Db2 (Shi et al., 2021), and (iii) Db3¹. To aid in the removal of non-Symbiodiniaceae sequences (e.g., non-target dinoflagellates), default RDP bootstrap value of 50 was used. The rank was set “unassigned” below this threshold, and these were hence removed from further analysis. The defined Symbiodiniaceae ASV table was utilized for downstream analysis, and abundance variations of Symbiodiniaceae genera and subtypes were analyzed.

The intragenomic variations (IGVs) among ITS2 regions challenged the Symbiodiniaceae diversity estimation. It is therefore important to determine the IGV profiles. The IGV profile for the Symbiodiniaceae diversity from the investigated samples was determined by SymPortal (Hume et al., 2019).

¹https://raw.githubusercontent.com/nitschkemathew/Symbiodatabaceae/master/Combining_databases/ITS2dbn1_Dinophy_Symbio.fasta

For the SymPortal analysis, all sets of sequences were remotely submitted to SymPortal.org. SymPortal identify the specific sets of defining intragenomic variants (DIVs) that are used to characterize ITS2-type profiles (Camp et al., 2020; Hume et al., 2020).

Statistical Analysis

The vegan package v.2.5-6 in R (Oksanen et al., 2018) was used to calculate the alpha-diversity indices such as ASV richness, Shannon, Chao, and Simpson indices and to prepare a rarefaction curve for the investigated samples. The significant differences among the diversity indices values were determined by the Kruskal-Wallis test (with Dunn’s *post hoc* test). Furthermore, the beta-diversity measures to test the statistical difference of Symbiodiniaceae community composition among the samples were determined by applying permutational multivariate analysis of variance (PERMANOVA) with 999 permutations using Bray-Curtis dissimilarity matrix in PRIMER v7 (Clarke and Gorley, 2015). Symbiodiniaceae community composition was ordinated using non-metric multidimensional scaling (nMDS), as implemented in vegan package in R using metaMDS function (Oksanen et al., 2018). Similarity percentage (SIMPER) analysis was performed to calculate the contribution of each ITS2 subtype to the dissimilarity within and between samples in the PRIMER v7. Analysis of similarity (ANOSIM) was carried out using 999 permutations with a Bray-Curtis distance in vegan package R

using Anosim function to test if there is a statistical difference between the Symbiodiniaceae communities of samples.

RESULTS

Diversity and Composition of Symbiodiniaceae Based on ITS2 Sequence Analysis

Deep sequencing analysis of ITS2 region recovered a total of 4,534,038 raw sequence reads from three compartment of the coral reef habitat, i.e., reef-building coral, bioeroding sponge, and seawater (**Supplementary File 1** and **Supplementary Table 1**). The raw amplicon sequencing dataset is available at the NCBI sequence read archive (SRA) database (accession PRJNA636097). After processing through DADA2 pipeline, the filtered sequence reads (3, 647, 450) were assigned to 1,008 unique ASVs (**Supplementary File 1** and **Supplementary Table 1**). The taxonomic classification of these ASVs showed high degree of variations when assigned against different Symbiodiniaceae databases investigated in this study. The ASVs with more than 50% confidence for their taxonomic assignments were 613, 594, 253 for the databases Db1, Db2, and Db3, respectively. The variations obtained at the genera level for the ASVs from different databases are shown in **Supplementary File 2** (**Supplementary Table 1**). The databases Db1 and Db2 showed similar results of taxonomic distribution and determined six Symbiodiniaceae genera (*Durusdinium*,

Gerakladium, *Symbiodinium*, *Cladocopium*, *Breviolum*, and *Fugacium*) (**Supplementary File 2** and **Supplementary Table 1**). However, Db3 showed the lowest ASVs (253), which were mainly assigned only to *Durusdinium*, *Gerakladium*, and *Symbiodinium* (**Supplementary File 2** and **Supplementary Table 1**). At ITS2-subtype level, Db1 and Db2 identified more Symbiodiniaceae diversity than Db3 (**Supplementary File 2** and **Supplementary Figures 1–3**). Based on the higher diversity determination, we followed the Db1 database sequences to represent Symbiodiniaceae diversity in our samples.

The assigned 613 Symbiodiniaceae ASVs further distributed as 174 for coral, 180 for sponge, and 464 in seawater. The overlap of these ASVs between coral, sponge, and seawater is shown in **Figure 2**. The distribution of these ASVs among the samples with sequencing reads was investigated with a rarefaction curve (**Supplementary File 1** and **Supplementary Figure 1**). Shannon's diversity index determined for the studied samples was in the order of seawater (3.24 ± 0.29) > *T. mesenterina* (2.46 ± 0.23) > *C. thomasi* (2.03 ± 0.40) (**Supplementary File 1** and **Supplementary Table 2**). A similar, trend was observed in the Simpsons index as seawater (0.92 ± 0.02) > *T. mesenterina* (0.85 ± 0.03) > *C. thomasi* (0.78 ± 0.06) (**Supplementary File 1** and **Supplementary Table 2**). The alpha-diversity indices determined were found significantly different only between coral and seawater based on the Kruskal-Wallis test, followed by Dunn's *post hoc* test ($p < 0.05$). The beta-diversity measures for the investigated samples showed significant differences among the composition of the Symbiodiniaceae community associated with the coral species *T. mesenterina* and the

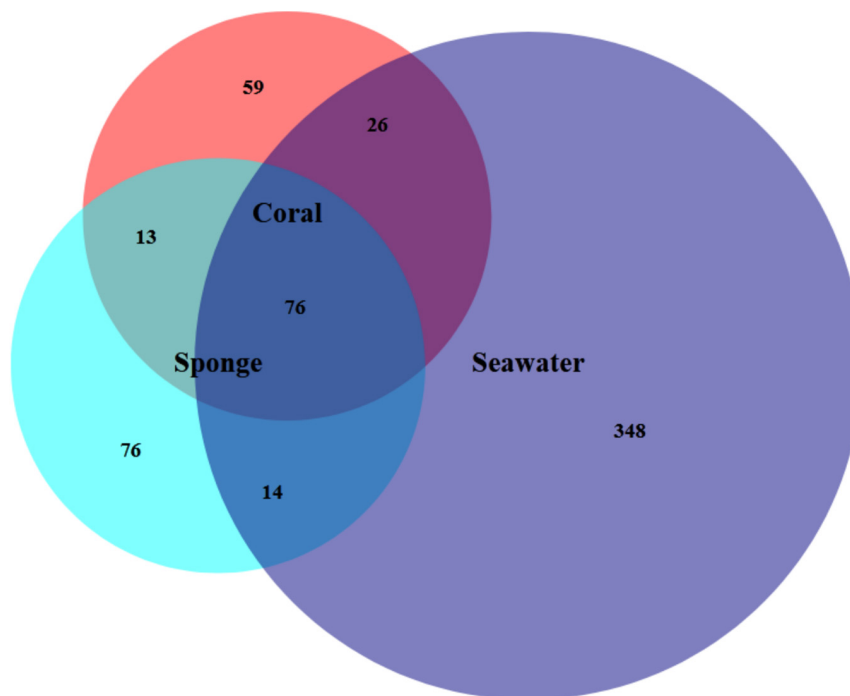


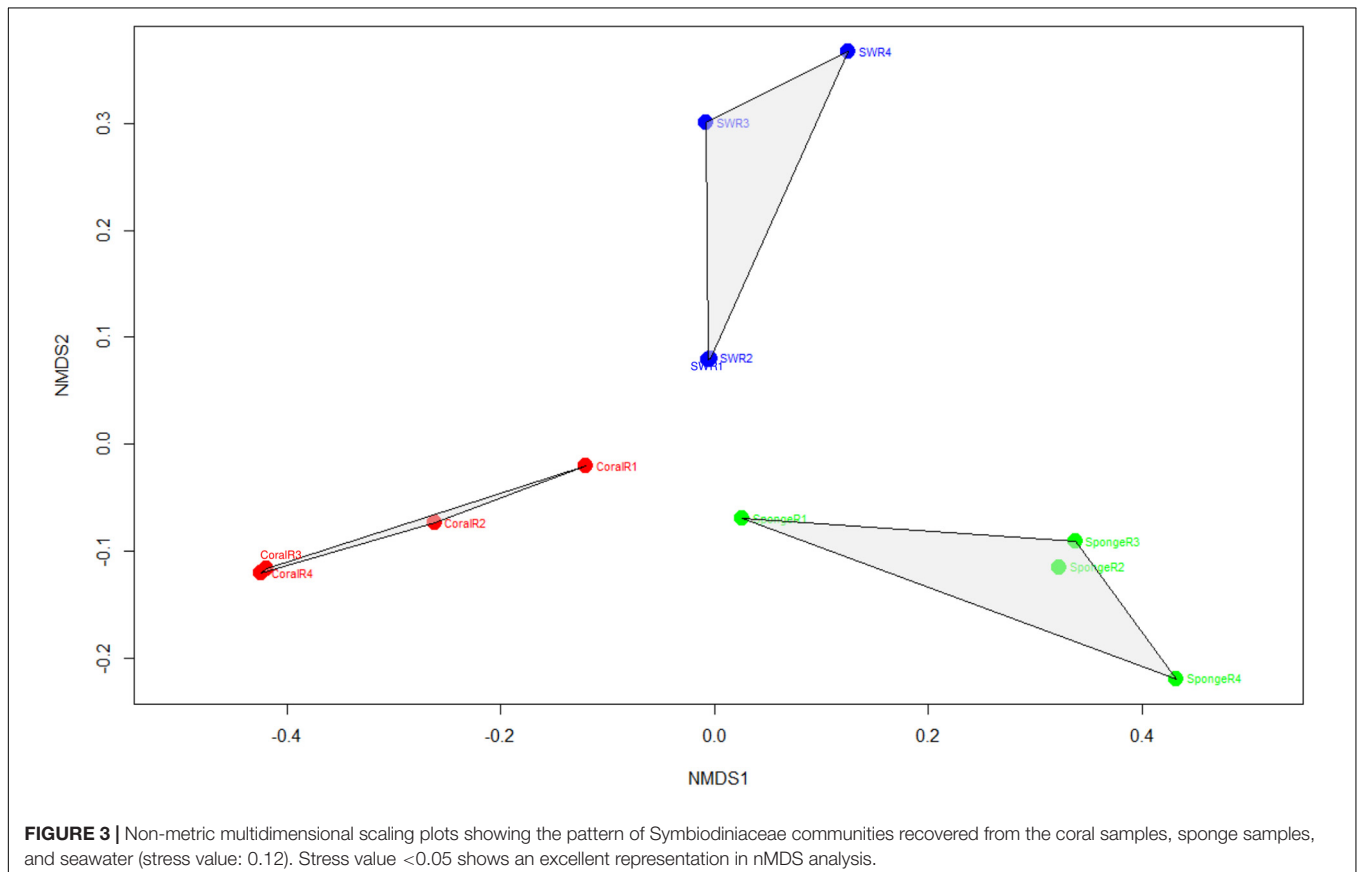
FIGURE 2 | Venn diagram shows the number of Symbiodiniaceae amplicon sequence variants (ASVs) present in each reef habitat compartment (coral, sponge, and seawater), as well as the amount of overlap between and among samples.

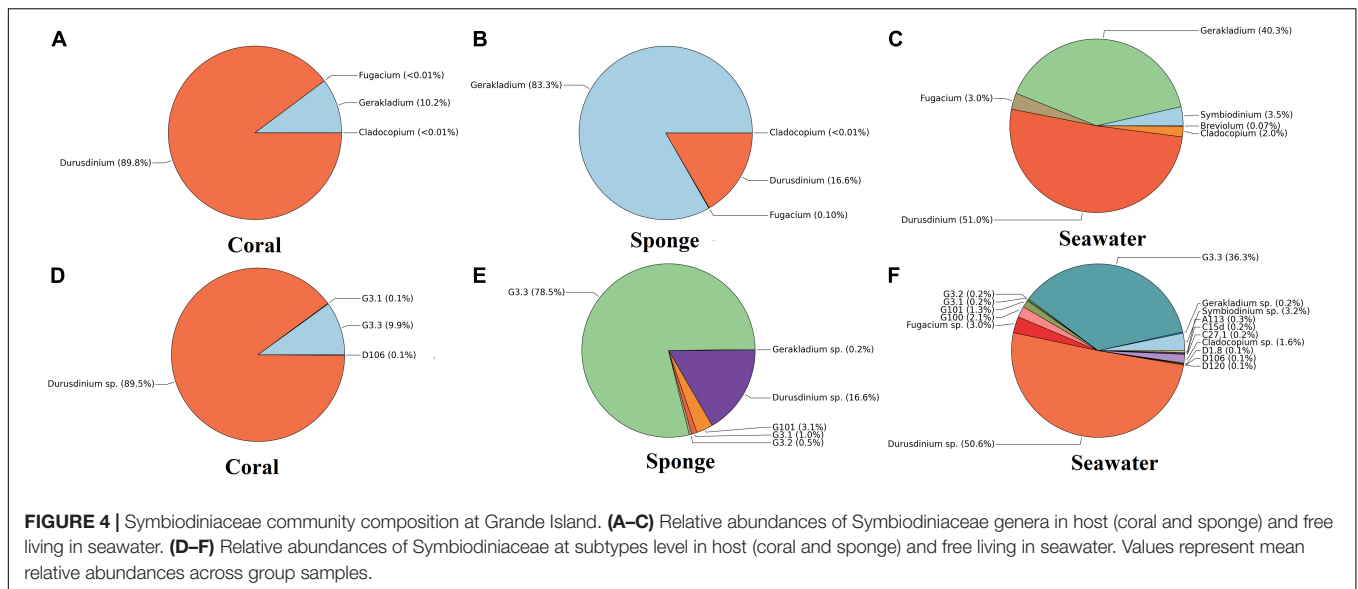
sponge species *C. thomasi* (PERMANOVA, $p = 0.04$; ANOSIM, $R = 0.854$, $p = 0.04$, see **Supplementary Tables 3, 4**). The Symbiodiniaceae communities between sponge-seawater and coral-seawater were also found to be significantly different (PERMANOVA and ANOSIM, $p < 0.05$, **Supplementary File 1** and **Supplementary Tables 3, 4**). The significant differences in beta-diversity between investigated coral and sponge species are mainly contributed by Symbiodiniaceae genus *Durusdinium* and *Gerakladium*. The results from the SIMPER analysis further confirmed higher dissimilarity in the Symbiodiniaceae community association between *T. mesenterina* and *C. thomasi* (average dissimilarity 58.3%) than *T. mesenterina*-seawater (average dissimilarity 42.4%) and *C. thomasi*-seawater (average dissimilarity 40%) (**Supplementary File 1** and **Supplementary Table 5**). The differential Symbiodiniaceae association was further confirmed by the clustering pattern obtained from nMDS analysis. The investigated host types were clustered distinctly and separately based on their associated Symbiodiniaceae community (**Figure 3**). The observed distinct variation among the Symbiodiniaceae species assemblage in bioeroding sponge and coral indicates the symbiont selectivity among two different hosts within the same reef habitat.

The most abundant Symbiodiniaceae genus found in the investigated coral species was *Durusdinium* ($89.8 \pm 11.7\%$), followed by *Gerakladium* ($10.2 \pm 11.7\%$) (**Figure 4A**). At ITS2 subtype level, *Durusdinium* sp. ($89.1 \pm 13.4\%$) was found

to be the dominant, followed by G3.3 ($9.9 \pm 12.9\%$) in the coral species *T. mesenterina* (**Figure 4D**). The other types of *Durusdinium*, i.e., D1.8, D105, D106, D120, D124, and D2 were detected in lower abundance (**Figure 4D**). On the contrary, the sponge species *C. thomasi* contained a higher abundance of *Gerakladium* ($83.3 \pm 23.7\%$), followed by *Durusdinium* ($16.6 \pm 23.8\%$) (**Figure 4B**). Among *Gerakladium* types, the highest dominance determined was for *Gerakladium* G3.3 ($78.5 \pm 21.2\%$), followed by *Durusdinium* D1 ($16.6 \pm 23.7\%$) (**Figure 4E**). The other types of *Gerakladium* G100, G101, G3.1, and G3.2 were detected in lower abundance (**Figure 4E**). The most abundant Symbiodiniaceae taxa in seawater samples were *Durusdinium* ($51.0 \pm 10.1\%$) and *Gerakladium* ($40.3 \pm 3.3\%$), followed by *Symbiodinium* ($3.5 \pm 5.5\%$), *Fugacium* ($3.0 \pm 3.1\%$), and *Cladocopium* in ($2.0 \pm 3.5\%$) (**Figure 4C**). *Breviolum* was also detected in seawater in a very low abundance ($<1\%$). Furthermore, at the ITS2 type level, seawater contained *Durusdinium* sp. ($50.6 \pm 13.9\%$) and *Gerakladium* G3.3 ($36.3 \pm 5.1\%$) (**Figure 4F**).

In order to define the intragenomic variants for the ITS2 region, SymPortal DIV profiles for the Symbiodiniaceae community in corals, sponge, and free-living habitats were determined. SymPortal analysis provided the complete ITS2 profile only for coral samples, which showed the dominance of ITS2 type profile D1 and lower dominance of types D4-D4c-D1c-D2-D6 (**Supplementary File 2** and **Supplementary Figure 4**).





However, seawater and sponge samples could not show the complete ITS2 type profiles (**Supplementary File 2** and **Supplementary Figure 5**).

DISCUSSION

This study determined the Symbiodiniaceae diversity associated with the two space competitors (i.e., coral and sponge) in the same reef habitat using high-throughput sequencing of the ITS2 region. ITS2 marker is commonly used to analyze Symbiodiniaceae (Thornhill et al., 2007; Stat et al., 2011; Shi et al., 2021). The present study followed the ASV-based approach for defining the Symbiodiniaceae diversity over the conventional operational taxonomic units (OTUs) using 97% similarity clustering threshold to collapse sequence diversity into OTUs. The redundancy in ITS2 delineation has been well documented based on the reference database employed (Tonk et al., 2013; Shi et al., 2021). This study confirms the variations in ITS2 delineation and taxonomic assignment through three different reference databases. The difference in the results obtained may be attributed to the sequence length and ITS2 boundary variations in the databases. Furthermore, this study confirms the IGV level delineation called as DIVs for ITS2 subtypes using SymPortal. The DIV profiles to search for Symbiodiniaceae community of coral showed strong overlap with the sponge and free-living habitat due to the high relative abundance of *Durusdinium* (D1) (**Supplementary File 2** and **Figure 3**).

Symbiodiniaceae Community Associated With the Coral *T. mesenterina*

The investigated coral *T. mesenterina* showed a higher abundance of the genus *Durusdinium*. Interestingly, *Durusdinium* genus is widely known to be associated with scleractinian corals from the Caribbean and Indo Pacific reefs (Knowlton and Rohwer, 2003; Jones et al., 2008; Brenner-Raffalli et al., 2018).

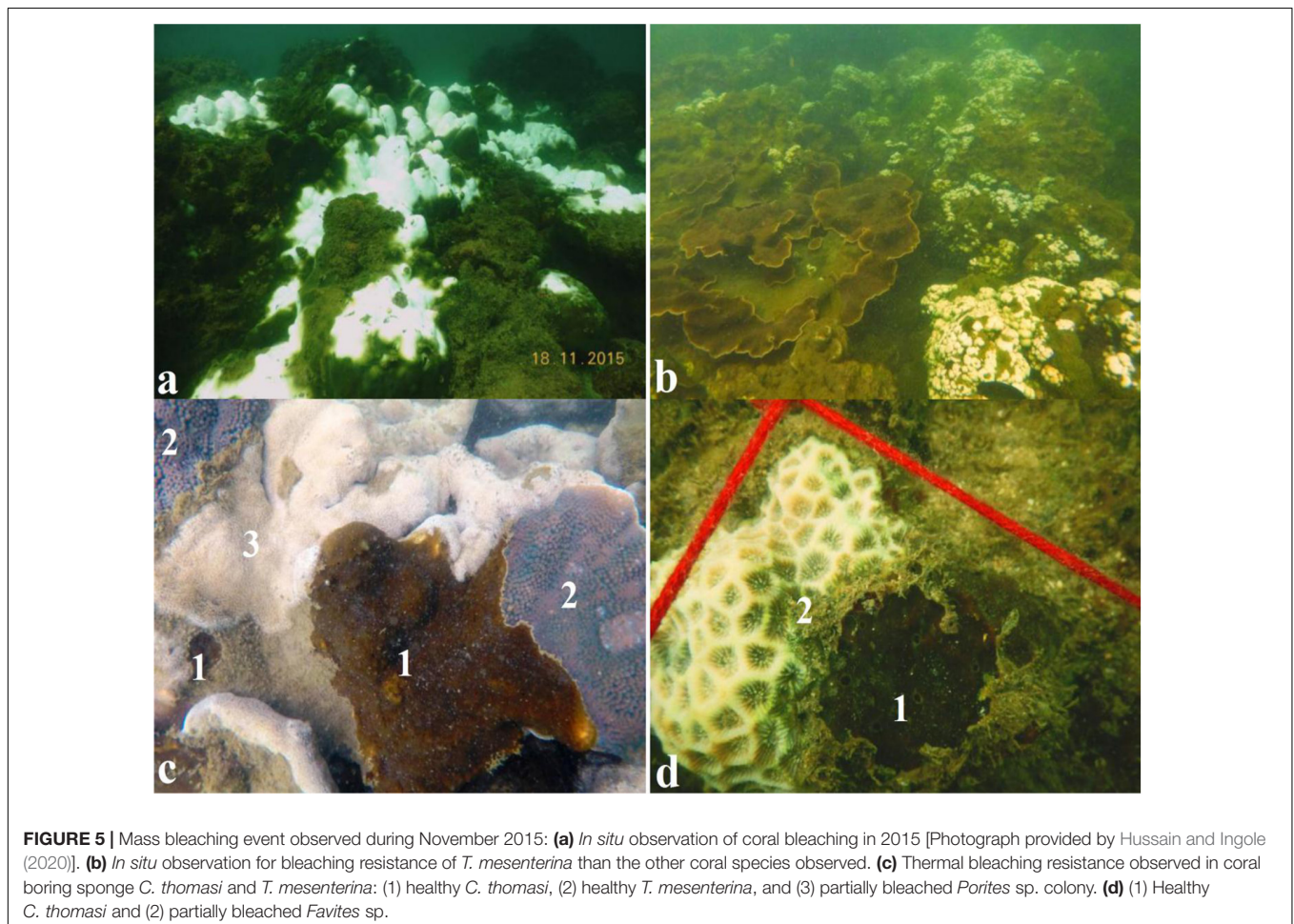
Previous studies have suggested that the association of coral with *Durusdinium* may indicate local environmental stressors, such as high temperature, sedimentation, and light intensity (D'Angelo et al., 2015; Osman et al., 2020; Wall et al., 2020). Studies from different global reefs attribute the increased association of *Durusdinium* with corals to the adaptation against thermal stress (Oladi et al., 2019; Chankong et al., 2020; Williams and Patterson, 2020). *Durusdinium* communities in corals from the Andaman Sea with high host specificity were attributed to higher turbidity and high nutrient concentrations in the reef (LaJeunesse et al., 2010b). In general, the studies have confirmed that the *Durusdinium* type D1a or D1-4 (*Durusdinium trenchii*) are more frequently associated with corals in thermally challenged marginal habitats (Cooper et al., 2009; LaJeunesse et al., 2010a; Stat et al., 2013; Oladi et al., 2019; Qin et al., 2019; Williams and Patterson, 2020). *D. trenchii* is often referred to as an opportunistic symbiont which makes their association heterologous (Smith et al., 2017; Matthews et al., 2018).

The marginal coral reef of the present study was subjected to severe thermal stress-driven coral-bleaching events from 2014 to 2016. Sea surface temperature (SST) data of NOAA Coral Reef Watch (NOAA-CRW) platform revealed that the SST exceeded the thermal bleaching thresholds throughout the years 2015 to 2019 (**Supplementary File 1** and **Supplementary Figure 2**). The underwater field survey confirmed *in situ* coral bleaching during October 2014, April 2015, October 2015, and April 2016 (Hussain and Ingole, 2020). The years 2014–2017 were the warmest years in history, leading to mass coral mortalities globally (Eakin et al., 2019; Skirving et al., 2019). There have been reports of coral bleaching in all major reefs of India during this period (Hussain and Ingole, 2020). Such warming events in the last few decades have significantly altered the coral population and led to the emergence of non-reef-forming communities (Hughes et al., 2017; Lough et al., 2018). This clearly implies that temperature and local stressors remain important drivers of coral decline; therefore, the response of Symbiodiniaceae to

stressors is crucial for predicting the response of the reef community as a whole.

Our *in situ* surveys confirmed high bleaching resilience in *T. mesenterina* (Figures 5a–c) while other coral genera such as *Coscinaria*, *Goniopora*, and *Porites* were susceptible to thermal bleaching (Supplementary File 1 and Supplementary Figure 3). The determined association of stress-tolerant Symbiodiniaceae members belonging to *Durusdinium* with the coral *T. mesenterina* may be attributed to its stress tolerance and bleaching resistance. A detailed analysis of Symbiodiniaceae association with other coral species though is needed to confirm the thermal-tolerance adaptation of *T. mesenterina*. Increased stress on marginal reefs tends to shift the coral community toward low species heterogeneity and to increase the dominance of species well adapted to increasing temperature regime (van Woesik et al., 2011; Hoegh-Guldberg et al., 2019). The switching of endosymbiont from *Cladocopium* to *Durusdinium* has been reported in adults of *Acropora millepora* in response to heat stress and, more recently, in *Acropora* spp. from Palk Bay (India) after the bleaching event in 2016 (Thinesh et al., 2019). In the disturbed reefs in Singapore, the higher bleaching resilience of *Pocillopora* was attributed to its association with thermotolerant *Durusdinium* (Guest

et al., 2016). The coral *Galaxea fascicularis* from the South China Sea was found to be more resistant to thermal stress because of its association with *Durusdinium* D1a (Zhou et al., 2017). In another report, *Pocillopora verrucosa* associated with *Durusdinium* D1a was found to be more resistant to thermal stress than *Pocillopora lutea* associated with *Cladocopium* (Qin et al., 2019). Interestingly, a decadal study with higher temperature variability in the Kenyan reef found that *Pavona* and *Pocillopora* were resistant to bleaching due to their association with *Durusdinium* (McClanahan et al., 2015). Similar results of higher temperature regime tolerance were reported for scleractinian coral *Leptoria phrygia* from Southern Taiwan (Carballo-Bolaños et al., 2019). Studies revealed that under high-temperature stress, *Durusdinium* D1a increases the coral bleaching thresholds by 1.0 to 1.5°C (Berkelmans and Van Oppen, 2006; Silverstein et al., 2015) by maintaining a high photochemical efficiency compared with *Breviolum* and *Cladocopium* (Cunning et al., 2017; Kluefer et al., 2017). Therefore, our observations suggest that *T. mesenterina* is tolerant against the thermal bleaching events in the studied marginal reef habitat. Our finding implies that the higher thermal resilience in *T. mesenterina* was possibly due to the association with *Durusdinium*. A similar association of *Durusdinium* with



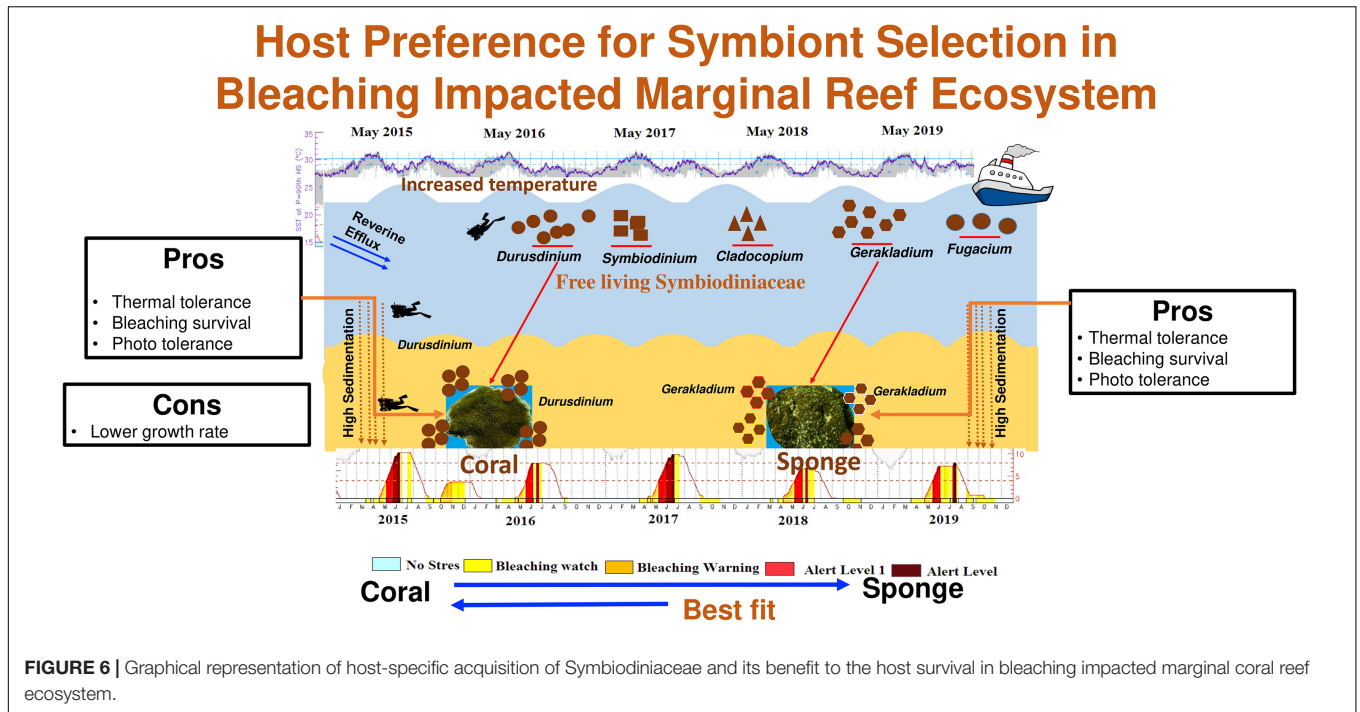


FIGURE 6 | Graphical representation of host-specific acquisition of Symbiodiniaceae and its benefit to the host survival in bleaching impacted marginal coral reef ecosystem.

T. mesenterina has been reported from the stressed marginal habitat of Taiwan (Chen et al., 2005).

Along with *Durusdinium*, *Gerakladium* (10.2%) was the subdominant genera in *T. mesenterina*. The association of *Gerakladium* with scleractinian coral is rare though a few studies reported its association with *Porites lobata* in Hawaii (Stat et al., 2013), *Orbicella annularis* from Virgin Islands (Edmunds et al., 2014; Pochon et al., 2014a), *Acropora* sp. from Western Australia (Thomas et al., 2014), and *Diploastrea heliopora* from the Great Barrier Reef (Chakravarti and van Oppen, 2018). *Gerakladium* is mostly associated with the specific group of sponges (Schönberg and Loh, 2005; Hill et al., 2011), soft corals (Van Oppen et al., 2005), and foraminifera (Pochon et al., 2014b). The simultaneous occurrence of *Durusdinium* and *Gerakladium* was reported in thermally tolerant *Porites lutea*, from the South China Sea (Qin et al., 2019). However, the *Gerakladium* association with *T. mesenterina* needs to be ascertained by increasing the range of study sites from different geographical locations.

Symbiodiniaceae Community Associated With the Sponge *C. thomasi*

The present study confirmed the dominance of *Gerakladium* in the encrusting sponge species *C. thomasi* unlike the dominance of *Durusdinium* in host coral *T. mesenterina*. The results indicated the host-specific association of Symbiodiniaceae members. The species-specificity and flexibility in the Symbiodiniaceae association have also been reported in some sponges (Hill et al., 2011; Ramsby et al., 2017). For instance, Caribbean clonoid species *C. aprica*, *C. laticavicola*, and *C. tenuis* are known to associate with *Symbiodinium* and *Breviolum*, while

the other member of the family *C. caribbaea*, *C. varians*, and *C. tumula* are known for their multi symbiont association with *Gerakladium*, *Symbiodinium*, or *Breviolum* (Granados et al., 2008; Hill et al., 2011; Ramsby et al., 2017). The Indo-Pacific *Cliona orientalis* is known to harbor only *Gerakladium* (Hill et al., 2011).

The Symbiodiniaceae of sponges were studied earlier using Symbiodiniaceae-specific markers based on Sanger sequencing approach or denaturing gradient gel electrophoresis (DGGE) methods (Schönberg and Loh, 2005; Granados et al., 2008; Hill et al., 2011; Pochon et al., 2014b; Ramsby et al., 2017, 2018) and a study by Ramsby et al. (2018) by NGS. The available literature suggests the wide occurrence of *Gerakladium* genus in *C. viridis* species complex, but there is less information about cryptic species or subtypes of Symbiodiniaceae (Supplementary File 1 and Supplementary Table 6). At the subtype level, only G2.1 was reported from the sponge *C. orientalis*. In the present study, we have utilized the high-throughput sequencing of the ITS2 region, which improved the detection of different Symbiodiniaceae subtypes from mixed populations and also determined community composition in the sponge. Within sponge *C. thomasi* samples, type G3.3 had the highest relative abundance (78.5%) followed by G101 (3.0%). In addition, the results detected type G3.1 and G3.2 at lower abundance (<1%), which indicates genetically distinct Symbiodiniaceae taxa in sponges. The advancement in detecting relatively rare Symbiodiniaceae subtypes reveals that sponge symbiont association can be flexible or specific within the same genus at the subtype level. The lower abundance of Symbiodiniaceae subtypes is known to play a significant role in coral holobiont resilience and response to perturbation (Ziegler et al., 2018). Therefore, the findings presented here

indicate that there are additional sponge-associated species within *Gerakladium* genus which prove the great importance of the way that ITS2 sequence data are analyzed and interpreted in studies concerning the biological diversity. The knowledge of the dinoflagellate communities associated with bioeroding sponges is limited at the species level, with only two known species (*Gerakladium endoclionum* from *C. orientalis*, and *Gerakladium spongiolum* from *C. varians*) from sponges (Ramsby et al., 2017). Our ITS2 rDNA based analysis could not confirm the species identity of Symbiodiniaceae associated with *C. thomasi* due to lack of species-specific subtypes information in the revised taxonomy of *Gerakladium* (LaJeunesse et al., 2018).

Different studies have confirmed the ecological significance of *Gerakladium* in the bioerosion capabilities, survival, and growth rate of Clionaid sponges (Fang et al., 2016, 2018a; Achlatis et al., 2019). Furthermore, Chakravarti and van Oppen (2018) showed the *Gerakladium* genus as thermotolerant by *ex situ* analysis. Our *in situ* observations indicated the increased prevalence of *C. thomasi* from 6% in 2015 to 11% in 2017 (**Supplementary File 1** and **Supplementary Figure 4**) and bleaching resistance during mass bleaching events (**Figures 5c,d**). The thermal tolerance of sponges during mass bleaching events may be attributed to its association with *Gerakladium*.

Environmental Acquisition of Symbiodiniaceae

Symbiodiniaceae communities of the ambient seawater were predominantly represented by *Durusdinium* and *Gerakladium*, while *Symbiodinium*, *Fugacium*, and *Cladocopium* in were less dominant in the present study. Water column Symbiodiniaceae community may be exclusively free-living or symbiotic with different benthic hosts (Yamashita and Koike, 2013; Nitschke et al., 2016; Claar et al., 2020). Most of corals (~80–85%) tend to acquire different symbionts from the surrounding environment at different life stages (Stat et al., 2008; Boulotte et al., 2016). The determined higher abundance of *Durusdinium* sp. in *T. mesenterina* and in ambient seawater (equal to *Gerakladium*) from the thermally challenged marginal sites indicates two possibilities of their association: (1) that the symbiont population in coral may have been retrieved from seawater or (2) the symbiont is typically associated with the coral hosts (Claar et al., 2020). Since horizontal acquisition is well established in corals, the former possibility appears a better fit. Unlike corals, vertical transmission of Symbiodiniaceae has been suggested in few sponges (Mariani et al., 2000, 2001). However, a few studies also suggested the environmental acquisition of free-living photosymbiont in sponges (Strehlow et al., 2016; Francis and Cleary, 2019). Also, it has been experimentally demonstrated that *C. varians* acquire symbiont from the ambient environment (Riesgo et al., 2014). The present study revealed the dominance of *Gerakladium* G3.3 in the sponge samples and also in ambient seawater.

Therefore, it can be inferred that there is a possibility for the acquisition of free-living symbiont from the ambient environment by *C. thomasi*, although detailed studies are

required to understand their mode of acquisition. Our results support the possibility of host-specific acquisition of photosymbionts as *Durusdinium* in coral and *Gerakladium* in the sponge (**Figure 6**). Host-specific Symbiodiniaceae association in coral is well noted from different bioregions (Bernasconi et al., 2019; Howe-Kerr et al., 2020; Wall et al., 2020). The differential acquisition of symbionts by different hosts from the same environment can be attributed to various factors such as (1) cellular signaling to and from host and symbiont (Davy et al., 2012), (2) metabolic requisites of both the host and symbiont (Suggett et al., 2017), (3) microhabitat conditions of the host, (4) mode of transmission of the symbiont, i.e., horizontal or vertical (Stat et al., 2008), and (5) selection mediated reshuffling and/or re-switching of symbiont (Boulotte et al., 2016). Nevertheless, physiological, molecular, genetical, and signaling related detailed studies are needed to confirm the mode of host-specific Symbiodiniaceae association.

CONCLUSION

The present study provides an important insight into the coral-Symbiodiniaceae-sponge symbiosis in a data-deficient marginal coral reef habitat. Our results unveil a high abundance of thermal stress-tolerant Symbiodiniaceae *Durusdinium* and *Gerakladium* in an ambient environment experiencing severe temperature anomalies for the last 5 years. Furthermore, the study showed differential associations of Symbiodiniaceae between two hosts indicating a host-specific mode of selection. Since both the dominant Symbiodiniaceae members are well known for their thermotolerance, the determined thermal resistance by both the hosts in this habitat may be attributed to their association with the resistant Symbiodiniaceae *Durusdinium* and *Gerakladium*. Hence, the study highlights the influence of *Durusdinium* and *Gerakladium* and their possible role in enhanced acclimatization capacity of coral *T. mesenterina* and bioeroding sponge *C. thomasi* in a suboptimal environmental regime. At large, the stress-tolerant symbiont association may increase the resistance of few species and aid their survival, thereby increasing their dominance in space competition. Further studies on physiological, metabolic, and transcriptomic insights will help confirm the energetic tradeoffs by symbiont communities in the success of their respective hosts.

SAMPLING AND FIELD STUDIES

The authors have obtained all necessary permits for sampling and field observation from the competent authorities.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and

accession number(s) can be found below: Nucleotide sequences have been submitted to the NCBI database under Bio project ID- PRJNA636097.

AUTHOR CONTRIBUTIONS

SM and VG conceptualized the study, designed the experiment, and analyzed the sequenced data. SM and KD performed sampling. SM performed DNA extraction experiments. KM performed the nMDS. AH did the field survey for bleaching and coral health assessment. MN, BI, and VG supervised the project and acquired the fund for the study. VG, SM, KD, and MN wrote the manuscript. KM and BI proofread the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.666825/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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