



Endosymbiotic *Symbiodinium* clades occurrence and influence on coral growth and resilience during stress

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Abstract

The endosymbionts of Symbiodiniaceae members establish an obligate relationship with most of the reef-building corals. Photosynthates of Symbiodiniaceae symbionts provide the maximum energy requirements of the host coral. Apart from the coral growth benefits, the mutual relationship extends to respond the environmental stress as well. Coral-endosymbiont mutualism is affected by various stress factors such as light, salinity, temperature, and eutrophication. However, the coral-algal symbionts adaptation to these rapid environmental changes is not much studied. Algal endosymbionts are classified into nine clades by genus level (major scleractinian corals – Clade A-D). These clades are named A to I with many sub-clades being presented in each clade that was identified based on the genetic marker ITS sequences, from which few are found tolerant to adverse conditions. This suggested that coral susceptibility or resistance to stress depends on the type of clade they harbor. Also, the prolonged environmental conditions may bring evolutionarily diverse clade lineages enabling corals to attain stress tolerance to temperature, UV, and high salinity. Thus, the present study may aid in understanding the coral-algal mutualistic adaptations under various stress conditions.

Keywords *Symbiodinium* · Evolution · Clades · Dinoflagellate · Endosymbiont

1 Introduction

Corals are sessile marine invertebrate animals that belong to Phylum cnidarian. Several polyps of coral form a colony and are generally classified as hard coral and soft coral. Their average tolerant level of environmental conditions such as temperature, salinity, nitrate, phosphate, and light is 21.7–29.6 °C, 28.7–40.4 PSU, 4.51 $\mu\text{mol L}^{-1}$, 0.63 $\mu\text{mol L}^{-1}$, and 450 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ respectively (Guan et al. 2015). Coral reefs formed by scleractinian corals provide shelter, food, and habitat for at least 25% of known marine species with rich biodiversity (Vanwonderghem and Webster 2020). Also, promotes an economic value of 30.1–37.5 billions USD per annum through coastal protection, tourism, and

fisheries (Moberg and Folke 1999; Saxena 2015; Reguero et al. 2018). Hence corals serve as food resources, and economic importance, and exhibit ecological services (Moberg and Folke 1999).

Photosynthetic dinoflagellates (*Symbiodinium*) of Reef corals live in the coral tissues and belong to the Symbiodiniaceae family commonly called Zooxanthellae. These dinoflagellates, form symbiosis with cnidarians such as corals, sea anemones, and jellyfish and would not exist freely in the external nutrient-poor water environment (LaJeunesse 2002). Corals and their algae hold a symbiotic association of mutualistic relationship by which both species get benefitted from each other (Suggett et al. 2017; Roth 2014). The photosynthetic components of zooxanthellae, such as glycerol, glucose, and amino acids are transferred to coral (Yellowlees et al. 2008). The corals assimilate these compounds like proteins, fats, and carbohydrates and produce calcium carbonate in the process of reef-building (Goreau et al. 1979). Through this symbiotic association, the endosymbiotic algae produce organic nutrients and transfer 95% of their energy to corals (Muscatine 1990). This photoautotrophic nutrition, performed by the endosymbiotic algae is of prime benefit to the coral host. This facilitates

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the inorganic carbon transport, which acts as a source of phosphate, nitrogen, and other inorganic nutrients through the host tissues. Thereby the symbiotic algae uptakes the metabolic breakdown products and CO₂ from corals (Yellowlees et al. 2008). Thus, the presence of *Symbiodinium* species reaching densities of about several million or more per square centimeter of coral tissue aids the survival, productivity, and success of their hosts (Muscatine and Porter 1977; LaJeunesse 2002; Yellowlees et al. 2008). At the same time, climate change, especially the temperature rise combined with human dependence on reef resources damage the coral–dinoflagellate interactions leading to coral decline worldwide. However, coral species are demonstrated for more tolerant of environmental stress with the capability of developing the adaptive features among all invertebrates and dinoflagellate symbiosis (Warner et al. 1996). Hence coral growth and productivity depend on the symbiosis with its endosymbiotic dinoflagellates also known as *Symbiodinium* (Muscatine 1990; Muscatine and Porter 1977; Yellowlees et al. 2008). Thereupon gathering the reported facts of the coral and its *Symbiodinium* is pivotal and this review majorly focuses on the various clades of *Symbiodinium* together with their merits to its coral host.

2 Coral and dinoflagellates

In highly oligotrophic conditions, the association between the photosynthetic dinoflagellates and corals is an important key to the growth of stony corals and reef ecosystem success (Ziegler et al. 2018). Corals provide a protected environment and CO₂ to algae for photosynthesis, and algae provide photosynthetic products for the coral to induce metabolic activity and cellular respiration (Suggett et al. 2017; Roth 2014). The symbiosis establishment between coral and algae was demonstrated through cellular signals such as MAMP-PRR (Microbe-Associated Molecular Pattern – Pattern Recognition Receptors) via algal glycan and host-lectin interaction (Davy et al. 2012). Cell surfaces of *Symbiodinium* clades A, B, D, E, and F were consistently identified with glycan residues *N*-Acetyl and mannose (Logan et al. 2010). Both the MAMPs are well characterized for their binding properties with PRR lectins (McGuinness et al. 2003). Similarly, three lectin types were identified with symbiotic corals such as *Montastraea faveolata* (Schwarz et al. 2008), *Sinularia lochomodes* (Jimbo et al. 2000), and *Ctenactis echinata* (Jimbo et al. 2010). Besides, PdC lectin from *Pocillopora damicornis* (Vidal-Dupiol et al. 2009) and millectin from *Acropora millepora* (Kvennefors et al. 2008) was elucidated for their putative involvement in symbiotic

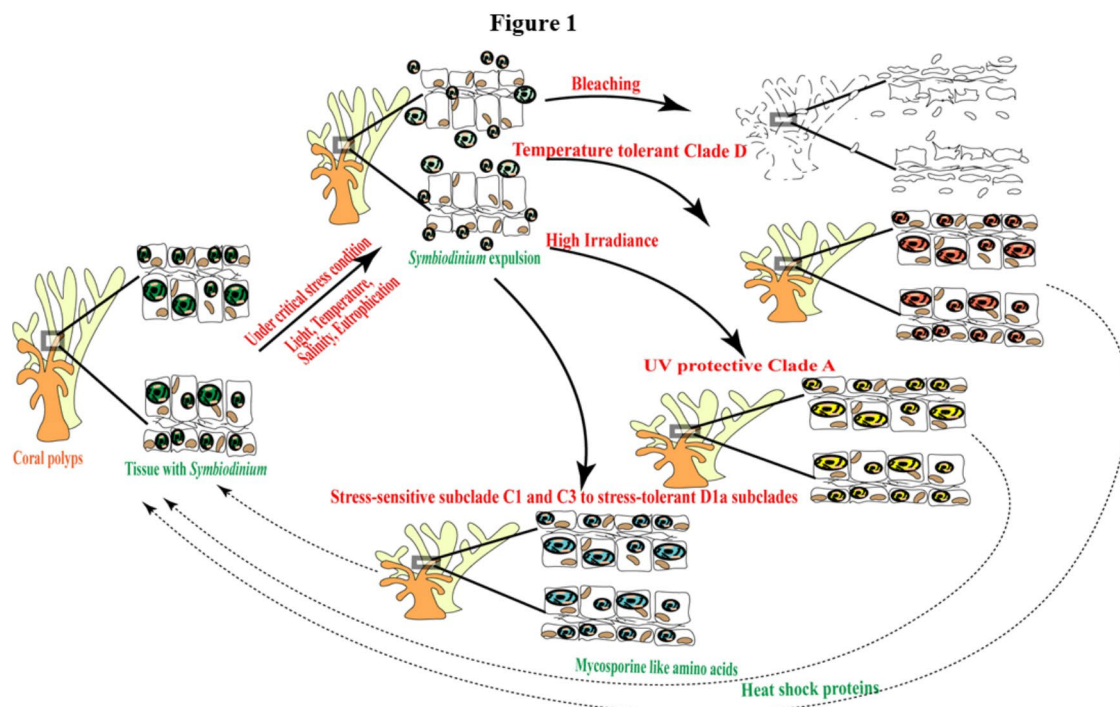


Fig. 1 The resilience of corals due to stress-tolerant *Symbiodinium* clades. The coral-associated *Symbiodinium* symbionts expel from the host due to critical stress conditions like high temperature, salinity, light, and eutrophication, which leads to bleaching and mortality. However, during these stress conditions, the stress-sensitive *Symbiodinium* clades are replaced by stress-tolerant clades such as Clade D (temperature tolerant), Clade A (UV protective), and subclade D1a (effluent sustenance) that helps in coral resilience

recognition Jimbo et al. 2000, 2010; Kvennefors et al. 2008; Schwarz et al. 2008; Vidal-Dupiol et al. 2009). However, cnidarians have several PRRs, apart from lectins such as Toll like receptors (TLRs), Nucleotide-binding oligomerization domain protein (NODs), scavenge receptors, and complement receptors as present in vertebrates, which could also involve in cnidarian-dinoflagellate symbiotic partnership (Davy et al. 2012). On account of these mutualistic symbiotic associations, the corals attain a high capacity to tolerate various environmental conditions (Silverstein et al. 2015). Also, the UV radiation exposures combined with thermal stress are been recognized as a major abiotic factor that leads to coral bleaching. In such instances, the mutualistic symbioses of photosynthetic dinoflagellates of some *Symbiodinium* clades act photoprotective by the synthesis of mycosporine-like amino acids (UV absorbing compound) (Fig. 1) (Hoegh-Guldberg and Jones 1999; Rosic and Dove 2011).

In Cnidarian-algal symbioses, the symbionts are transferred to the coral host, either by vertical or horizontal transmission with each new host generation (Barneah et al. 2004). Symbionts are directly carried from parent to offspring host through vertical transmission, while in horizontal, the host progeny acquires its symbiont from the surrounding environment (Barneah et al. 2004; Byler et al. 2013). That is, the coral larvae acquire their symbiont from the environment immediately after their substrate settlement and metamorphosis. Various researches of past decades had viewed that the *Symbiodinium* and coral host pairings are diverse (Ziegler et al. 2018). Also, rare cryptic *Symbiodinium* diversity contributes to coral for their potential functions that provide environmental resilience to coral holobiont (Ziegler et al. 2018). Likewise, a study from the northern red sea had noticed that the endosymbiotic algae are highly host-specific and exhibit high thermal tolerance even in extreme conditions in that region (Osman et al. 2020). These unicellular dinoflagellates are classified into 9 clades (A-I) with subclades of distinct phylogeny based upon their ribosomal chloroplast and nuclear genes (Pochon and Gates 2010; Pochon et al. 2006; Santos et al. 2002). Still every year, some aspects of *Symbiodinium* diversity are reported, confirming their genetic variations to be abundant and broad (LaJeunesse et al. 2018).

3 Factors affecting coral *Symbiodinium* and their response

Several of the planet's ecosystems are badly impacted due to rapid climate change, destructing various key ecological processes including primary production, respiration, energy, carbon and nutrient flow through food webs,

reproduction, and decomposition that affects organisms of broad range in diverse geographical distributions (Walther et al. 2002). Especially coral reefs are vastly affected due to their extreme sensitivity to prolonged UV stress, temperature stress, salinity, and eutrophication (Muscatine et al. 1998; Coles and Brown 2003; Fitt et al. 2001). Series of events that occur under UV stress include a decrease in the evolution of photosynthetic oxygen, Chlorophyll a, growth rate, carbon-nitrogen ratios, and Rubisco enzyme activity (Lesser 1996; Banazak and Trench 1995). Particularly temperatures of a few degrees higher involve significant loss of mutualistic dinoflagellates from coral tissues leading to coral bleaching (Jones and Berkelmans 2010; Porter et al. 1989). This phylogenetic incompatibility among the symbiont phylogenies and host had indicated that over evolutionary time scales such partnerships do change (Rowan and Powers 1991; LaJeunesse 2002). However, in coincidence with the adaptive radiations and persistent environmental conditions lasting for a thousand or millions of years, the *Symbiodinium* lineages (clades) of evolutionary divergent had acquired ecological dominance, as suggested by global phylogeographic patterns (Rowan and Powers 1991; LaJeunesse 2002). It is also been proposed that severe coral bleaching instances may hasten changes between coral populations so that individual colonies will take in thermal tolerant symbionts (Baker 2001; Baker et al. 2015). Thereupon, it was studied that *Symbiodinium* plays a major role in the adaptation of corals during rapid environmental changes. For example, the corals such as *Acropora* sp., *Galaxea fascicularis*, *Platygyra lamellina*, and *Sarcophyton glaucum* of the tropical and subtropical region of the northern south china were observed for their adaptation to environmental conditions (temperature and nutrient inflow) by changing *Symbiodinium* clades or subclades (Gong et al. 2018). To tolerate such environmental conditions, they take up a greater number of *Symbiodinium* clade D, which are thermal tolerant (Gong et al. 2018). *Symbiodinium* clade D is mostly found highly distributed in extremely hot regions (Berkelmans and Van Oppen 2006). Similarly, the corals ability in shuffling the *Symbiodinium* clades/types based on the environmental condition was observed in addition to the resistant *Symbiodinium* clades to overcome mainly seawater temperature fluctuations (LaJeunesse 2004a; Thornhill et al. 2006). Also, due to directional selection, new coral host *Symbiodinium* combinations may arise (Keshavmurthy et al. 2017). Likewise, the coral *Porites lutea* can also adapt to various environmental conditions through host-specific *Symbiodinium* subclades such as C15, C15.6, and C91. Also, under critical conditions such as in nuclear power plant effluents, the corals are observed to change their subclades of *Symbiodinium* from stress-sensitive subclades to stress-tolerant subclades (from C1 and C3 to D1a) (Keshavmurthy

et al. 2014). Although the shuffling of clades to the thermal tolerance is known, field studies have not yet clearly demonstrated the maximum spread of shuffling in a location, such as all corals have the ability to shuffle symbiont types or any ecological benefits due to the new addition of symbiont association with the host (Jones and Berkelmans 2010). However, experimental analysis in *Acropora millepora* on the growth rates measurement revealed that corals with D type symbionts grew slower than corals with C type symbionts due to the acclimatization process to the warmer conditions by changing to more thermally tolerant type D (Jones and Berkelmans 2010).

The Symbiodiniaceae association is influenced by depth as well which is appeared to be dependent on both region and coral species. In such instances, the shallow coral communities exhibit high dinoflagellate diversity than the samples beyond 16 m depths that were observed in Belize among the coral *Montastraea cavernosa*. Hence these symbionts might be depth specialized communities over the depths of 40–60 m (Eckert et al. 2020). Likewise, high salinity is observed to convey extraordinarily higher thermotolerance and with an increase in salinity, the bleaching severity is reduced in high saline environments like the Persian/Arabian Gulf (PAG) and Red sea which is dependent on specific host strain and symbiont type (Gegner et al. 2017). These corals from PAG are associated with *Symbiodinium thermophilum* which exhibits strong local adaptation to high temperature and exceptional high salinity and this heat tolerance is lost when the corals are exposed to low salinity levels (D'Angelo et al. 2015). Similar to other stress factors, the photobiology of four different *Symbiodinium* is also studied for photoacclimation and thermal stress. Where the *Symbiodinium* of clade F isolated from the coral *Meandrina meandrites* had exhibited great capacity of photoacclimation with growth at high temperature and light (Robison and Warner 2006).

4 *Symbiodinium* and clades in a scleractinian coral

Endosymbiotic algae *Symbiodinium* is classified into nine clades or groups by genus level by the development of molecular tools and next-generation sequencing. These clades are named A to I with many subclades being presented in each clade through the understanding of their taxonomic distribution which was identified based on the genetic marker ITS 2 sequences (Pochon and Gates 2010; Coffroth and Santos 2005). Among all the nine clades (A-I), the genus names were established recently to seven genera (A-G) (Leveque et al. 2019). The phylogenetic analysis of these *Symbiodinium* clades (A-G) are reported into seven genera based on their

molecular, morphological, physiological, and ecological findings into *Symbiodinium* as clade A, *Breviolum* as clade B, *Cladocopium* as clade C, *Durusdinium* as clade D, *Effrenium* as clade E, *Fugacium* as clade F and *Gerakladium* as clade G (LaJeunesse et al. 2018). A majority of these clades such as clades A, B, C, and D (Table 1) are associated with the hard corals (Liu et al. 2018). Among them clades A to D, are majorly found in the scleractinian coral, clade E is found in Anemone (*Anthopleura elegantissima*), clade F is found in foraminifera (*Sorites* sp., *Amphisorus hemprichii*, *Montipora verrucosa* and *Marginopora* sp.) and rarely in scleractinian coral (*Alveopora japonica*), clade G is present in foraminifera (*Sorites* sp., *Marginopora vertebralis*. and *M. kudakajimaensis*), sponges (*Cliona orientalis*), octocoral (*Junceella fragilis*, *Euplexaura nuttingi* and *Stereonephthya* sp.) and rarely distributed in hard coral (*Stylophora pistillata*) and clade H (*Sorites* sp. and *Amphisorus* sp.) are found only in foraminifera (Pochon and Pawlowski 2006; Pochon et al. 2007). Each clade can be located in its particular environment conditions for instance clade A and B mostly prefers to locate in shallow-water corals (Chen et al. 2003), clade C abundantly occurs in greater depths and photic zones (Innis et al. 2018), and clade D is mainly located in the places of high thermal conditions (Thronhill et al. 2005; Chen et al. 2003). Thus, among all the endosymbiotic clades discussed, the genus *Cladocopium* (Clade C) is highly distributed around the reef environments LaJeunesse 2001; Magalon et al. 2007; Lien et al. 2012; Yang et al. 2012; Tong et al. 2014) (Table 1). Besides, the spatial and geographic distribution also determines the coral-algal association (Tan et al. 2020). For example, *Symbiodinium* (clade A), *Breviolum* (clade B), and *Fugacium* (formerly clade F) are more prevalent at higher latitudes, while *Cladocopium* (Clade C) is dominant in tropical Eastern-Pacific regions (Baker and Rowan 1997), while across the Caribbean *Breviolum* is dominant but rare or absent in the Indo-Pacific (Lewis et al. 2018).

Interestingly, more than one clade or subclade is also observed in one individual host (Table 2). The coral host *Platygyra daedalea* is found to harbor more than one clade such as clades A, B, and C in their tissues of samples collected in April, May, and July 2008 from the inshore and offshore reefs of the north of the Arabian Gulf (Mahmoud and Sarraf 2016). But Reports from inshore and offshore reef systems in Kuwait showed that *P. daedalea* suffered 100% damage in response to temperature, while the other coral species reported damages between 20 and 97% (Mahmoud and Sarraf 2016). Also, in the temperate region of Japan, the genotype clades C and D are harbored in coral *Oulastrea crispata* (Faviidae family) and the coral *Alveopora japonica* is observed to harbor clades C and F (Poritidae family). Thereby, clade C was found to dominate over 58 coral species of the region (Lien et al. 2012). In the Pacific, corals

Table 1 Distribution of some *Symbiodinium* clades in scleractinian coral hosts around the world

Clade	Location	Host	Reference
<i>Symbiodinium</i> A	Caribbean and Eastern pacific tropical region	<i>Acropora cervicornis</i> , <i>A. palmata</i> , <i>Porites astereoides</i> , <i>P. furcata</i> , <i>P. colonensis</i> , <i>Stephanocoenia intercepta</i> , <i>S. michelinii</i> , <i>Montastraea annularis</i> , <i>M. faveolata</i>	Baker and Rowan 1997; LaJeunesse 2002
	Indo pacific	<i>Scapophyllia cylindrical</i> <i>Goniastrea</i> spp	Leveque et al. (2019)
	Southeast Asia	<i>Porites lutea</i>	Tan et al. (2020)
	North of the Arabian Gulf	<i>Platygyra daedalea</i>	Mahmoud and Sarraf (2016)
	Great Barrier Reef (GBR)	<i>Acropora</i> spp, <i>Millepora platyphylla</i> , <i>Pocillopora damicornis</i>	Tonk et al. (2014)
	Chagos Archipelago - Central Indian Ocean	<i>Isopora palifera</i> , <i>Acropora muricata</i>	Yang et al. (2012)
<i>Breviolum</i> B	Caribbean and Eastern pacific tropical region	<i>Cladocora arbuscula</i> , <i>Colpophyllia natans</i> , <i>Dendrogyra cylindrus</i> , <i>Diploria clivosa</i> , <i>D. strigosa</i> , <i>D. labyrinthiformis</i> , <i>Eusmilia fastigiata</i> , <i>Favia fragum</i> , <i>Madracis decactis</i> , <i>M. mirabilis</i> , <i>M. formosa</i> , <i>Manicina aereolata</i> , <i>Meandrina meandrites</i> , <i>Siderastrea radians</i> , <i>Porites astereoides</i> , <i>P. furcata</i> , <i>Montastraea annularis</i> , <i>M. faveolata</i>	Baker and Rowan 1997; LaJeunesse 2002
	North of the Arabian Gulf	<i>Porites astereoides</i> , <i>P. furcata</i> , <i>Montastraea annularis</i> , <i>M. faveolata</i> <i>Platygyra daedalea</i>	Mahmoud and Sarraf (2016)
<i>Cladocorium</i> C	Caribbean and Eastern pacific tropical region	<i>Agaricia agaricites</i> , <i>A. fragilis</i> , <i>A. humilis</i> , <i>A. tenuifolia</i> , <i>A. lamarcki</i> , <i>A. danae</i> , <i>Acropora cervicornis</i> , <i>Colpophyllia natans</i> , <i>Eusmilia fastigiata</i> , <i>Favia fragum</i> , <i>Colpophyllia natans</i> , <i>Diploria strigosa</i> , <i>D. labyrinthiformis</i> , <i>D. clivosa</i> , <i>Isophyllastrea rigida</i> , <i>Isophyllia sinuosa</i> , <i>Leptoseris cucullata</i> , <i>Manicina aereolata</i> , <i>Montastraea cavernosa</i> , <i>M. faveolata</i> , <i>M. annularis</i> , <i>Mycetophyllia danaana</i> , <i>M. lamarckiana</i> , <i>M. ferox</i> , <i>Porites colonensis</i> , <i>P. asteroids</i> , <i>Porites divaricata</i> , <i>P. furcata</i> , <i>P. porites</i> , <i>P. lobata</i> , <i>P. panamensis</i> , <i>Siderastrea siderea</i> , <i>Scolymia cubensis</i> , <i>Stephanocoenia michelinii</i> , <i>Pocillopora damicornis</i> , <i>P. elegans</i> , <i>P. eydouxi</i> , <i>Psammocora stellata</i> , <i>P. superficialis</i> , <i>Pavona gigantea</i> , <i>P. clavus</i> , <i>P. varians</i> , <i>Gardineroseris planulata</i>	Baker and Rowan 1997; LaJeunesse 2002
	Indo Pacific	<i>Pavona duerdeni</i> , <i>Hydnophora exesa</i> , <i>Acanthastrea</i> spp, <i>Pocillopora damicornis</i>	Leveque et al. (2019)
	Japan (30°–35°N)	<i>Acropora</i> spp, <i>Montipora</i> spp, <i>Pavona cactus</i> , <i>P. decussate</i> , <i>Favia</i> spp, <i>Cyphastrea</i> spp, <i>Goniastrea</i> spp, <i>Leptastrea</i> spp, <i>Montastraea valenciennesi</i> , <i>Platygyra</i> spp, <i>Lithophyllon undulatum</i>	Lien et al. (2012);
	Southeast Asia	<i>Alveopora japonica</i>	Tan et al. (2020)
	Hawaii, Chagos Archipelago - French Polynesia, Okinawa – Japan	<i>Goniopora</i> spp, <i>Porites</i> spp <i>Psammocora</i> spp, <i>Coscinaraea</i> spp, <i>Echinophyllia aspera</i> , <i>Pectinia ayleni</i> , <i>Goniastrea</i> spp, <i>Merulina</i> spp, <i>Scapophyllia cylindrical</i> , <i>Porites lutea</i> , <i>Pocillopora</i> spp	Magalon et al. (2007)
	North of the Arabian Gulf	<i>Stylophora pistillata</i> , <i>Acropora</i> spp, <i>Porites compressa</i> , <i>Goniopora lobate</i> , <i>Psammocora contigua</i> , <i>Coscinaraea columna</i> , <i>Pavona decussate</i> , <i>Dipsastraea pallida</i>	Mahmoud and Sarraf (2016)
	Great Barrier Reef (GBR)	<i>Favites pentagona</i> , <i>Plesiastrea versipora</i> , <i>Cyphastrea microphthalma</i> , <i>Platygyra daedalea</i> , <i>Turbinaria pellata</i> , <i>Acropora</i> spp.	Little et al. (2004), Jones and Berkelmans (2010); Tonk et al. (2014)
	Tonk et al. (2014) compiled 26 studies on reef invertebrate- <i>Symbiodinium</i> clade associations on the GBR.	Clade C was very dominant and diverse (56 out of 62 types belonged to clade C) across the GBR	Tonk et al. (2014)
	Chagos Archipelago, Central Indian Ocean	<i>Isopora palifera</i> , <i>Acropora muricata</i> , <i>Pocillopora</i> spp, <i>Stylophora pistillata</i> , <i>Seriatopora hystrix</i>	Yang et al. (2012)
	Pratas Island, Northern South China sea	<i>Astreopora</i> , <i>Montipora</i> , <i>Acropora</i> , <i>Pachyseris</i> , <i>Pavona</i> , <i>Turbinaria</i> , <i>Oxypora</i> , <i>Cyphastrea</i> , <i>Hydnophora</i> , <i>Echinopora</i> , <i>Favia</i> , <i>Favites</i> , <i>Coelastrea</i> , <i>Astrea</i> , <i>Pectinia</i> , <i>Leptastrea</i> , <i>Fungia</i> , <i>Psammocora</i> , <i>Porites</i> , <i>Goniopora</i>	Keshavmurthy et al. (2017)
Nanwan, Kenting, Southern Taiwan	<i>Acanthastrea echinata</i> , <i>Acropora nana</i> , <i>Cyphastrea chalcidicum</i> , <i>C. microphthalma</i> , <i>Favia stelligera</i> , <i>Favites abdita</i> , <i>Galaxea fascicularis</i> , <i>Goniastrea retiformis</i> , <i>Isopora palifera</i> , <i>Leptoria phrygia</i> , <i>Montastrea valenciennesi</i> , <i>Montipora millepora</i> , <i>Pavona varians</i> , <i>Platygyra verweyi</i> , <i>Pocillopora damicornis</i> , <i>Porites lobata</i> , <i>Seriatopora caliendrum</i> , <i>Stylophora pistillata</i>	Keshavmurthy et al. (2014).	

Table 1 (continued)

Clade	Location	Host	Reference
<i>Durus-dinium</i> D	Caribbean Indo-Pacific	<i>Agaricia humilis</i> , <i>Montastraea faveolata</i> , <i>M. annularis</i> <i>Pocillopora elegans</i> , <i>Goniastrea</i> spp, <i>Merulina ampliata</i> , <i>Scapophyllia cylindrical</i>	LaJeunesse 2002 Leveque et al. (2019)
	Japan (30°–35°N)	<i>Oulastrea crispate</i>	Lien et al. (2012)
	Southeast Asia	<i>Porites lutea</i>	Tan et al. (2020)
	Great Barrier Reef	<i>Acropora</i> spp	Jones and Berkemans (2010); Tonk et al. (2014)
	Pratas Island, Northern South China sea	<i>Montipora</i> , <i>Acropora</i> , <i>Pachyseris</i> , <i>Pavona</i> , <i>Turbinaria</i> , <i>Oxypora</i> , <i>Cyphastrea</i> , <i>Hydnophora</i> , <i>Echinopora</i> , <i>Favia</i> , <i>Favites</i> , <i>Coelastrea</i> , <i>Astrea</i> , <i>Pectinia</i> , <i>Goniopora</i>	Keshavmurthy et al. (2017)
	Nanwan, Kenting, Sothen Taiwan	<i>Acanthastrea echinata</i> , <i>Acropora nana</i> , <i>Cyphastrea chalcidicum</i> , <i>C. microphthalma</i> , <i>Favia stelligera</i> , <i>Favites abdita</i> , <i>Galaxea fascicularis</i> , <i>Goniastrea retiformis</i> , <i>Isopora palifera</i> , <i>Leptoria phrygia</i> , <i>Montastrea valenciennesi</i> , <i>Montipora millepora</i> , <i>Pavona varians</i> , <i>Platygyra verweyi</i> , <i>Pocillopora damicornis</i> , <i>Porites lobata</i>	Keshavmurthy et al. (2014)

Table 2 Harboring multiple clades in single host (in some Scleractinian corals) -worldwide distribution

Host (Hard coral)	Clade	Location	References
<i>Platygyra daedalea</i>	A / B / C	North of the Arabian Gulf	Mahmoud and Sarraf 2016
<i>Oulastrea crispate</i>	C / D	Japan	Lien et al. 2012
<i>Alveopora japonica</i>	C / F		
<i>Pocillopora damicornis</i>	A / C1 / D	Pacific region	Magalon et al. 2007
<i>Agaricia humilis</i> ; <i>Colpophyllia natans</i> ; <i>Diploria strigose</i> ; <i>Eusmilia fastigiata</i> ; <i>Favia fragum</i> ; <i>Manicina aereolata</i> ; <i>Porites astereoides</i> ; <i>Porites furcate</i> ; <i>Montastraea annularis</i>	C3a / C1 / D1a; B6 / C1; B1 / C1; B1 / C1; B1 / C1; B1 / C1; A4a / A3 / B1; A4 / B1; B1 / C3	Caribbean	LaJeunesse 2002
<i>Montipora</i> , <i>Acropora</i> , <i>Pavona</i> , <i>Turbinaria</i> , <i>Oxypora</i> , <i>Cyphastrea</i> , <i>Echinopora</i> , <i>Coelastrea</i> , <i>Astrea</i> , <i>Pectinia</i> , <i>Goniopora</i>	C / D	Pratas Island, Northern South China sea	Keshavmurthy et al. (2017)
<i>Acanthastrea echinata</i> , <i>Acropora nana</i> , <i>Cyphastrea chalcidicum</i> , <i>C. microphthalma</i> , <i>Favia stelligera</i> , <i>Favites abdita</i> , <i>Galaxea fascicularis</i> , <i>Goniastrea retiformis</i> , <i>Isopora palifera</i> , <i>Leptoria Phrygia</i> , <i>Montastrea valenciennesi</i> , <i>Montipora millepora</i> , <i>Pavona varians</i> , <i>Platygyra verweyi</i> , <i>Pocillopora damicornis</i> , <i>Porites lobata</i>	a mixture of type 'C' (C1/C3/C21a/C15) and 'D' (D1a)	Nanwan, Kenting, Southern Taiwan	Keshavmurthy et al. (2014)
<i>Acropora valida</i> ; <i>Acropora tenuis</i> ; <i>A. valida</i> ; <i>A. nobilis</i> ; <i>A. millepora</i> ; <i>Pocillopora damicornis</i> ; <i>Turbinaria reniformis</i> , <i>Pocillopora damicornis</i> ; <i>Leptoria Phrygia</i> ; <i>Montastrea curta</i> ; <i>Hydnophora microconos</i> ; <i>Stylophora pistillata</i>	A / C3; C / D; C / D; C / D; C1/C3 and D; C1 / A; C1 / D; C1 / D; C3 / D1a; C3 / D1a; C3 / D1a; C8a / G	Great Barrier Reef (GBR), Australia	Tonk et al. (2014)

Pocillopora damicornis are harbored with subclade C1 and clade D, A (Magalon et al. 2007) (Table 2).

5 Symbiodinium and clades in octocorals

Worldwide tropical Octocorals are reported to harbor five *Symbiodinium* clades such as clades A, B, C, D, and G (Goulet et al. 2008) (Table 3). The clade identity of dinoflagellates in soft coral hosts (Eilat, Red sea) has been investigated in relation to their hosts mode of acquisition of symbionts (Barneah et al. 2004). That is, all hosts using vertical transmission distinctly harbored dinoflagellates belonging to clade A while those with horizontal transmission harbored

endosymbionts belonging to clade C (Barneah et al. 2004). Among the other clades, clade D can tolerate high thermal conditions. Based on their distribution among corals, *Symbiodinium* clade C is found to be more dominant than other clades of Symbiodiniaceae (LaJeunesse et al. 2018). Australian reefs are studied to hold higher diversity of *Symbiodinium* clade C than the other regions and a lower density of clade D is distributed together with some of clade G (Van Oppen et al. 2005). Likewise, a higher density of Clade B is distributed in the regions of Bahamas, Panama, and Mexico. Interestingly, in the reefs of Australia both clades C and D are harbored together in the same host species such as *Cladiella* spp and *Klyxum* spp. (LaJeunesse et al. 2004a; Van Oppen et al. 2005). Also, clades B and C are harbored by

Table 3 Distribution of some *Symbiodinium* clades in octo-coral hosts around the world

Clade	Location	Host	Reference
A <i>Symbiodinium</i>	Hawaii	<i>Anthelia</i> spp	Goulet et al 2008
	Australia	<i>Capnella</i> spp	Van oppen et al. 2005
	Israel	<i>Litophyton arboretum</i> , <i>Stereonephthya cundabiluensis</i>	Goulet et al 2008, Barneah et al. 2004, LaJeunesse et al. 2003
B <i>Breviolum</i>	Barbados	<i>Erythropodium caribaeorum</i> , <i>Briareum asbestinum</i> , <i>Gorgonia</i> spp, <i>Pseudopterogorgia</i> spp, <i>Muricea</i> spp, <i>Plexaura flexuosa</i>	Goulet et al. 2008, Goulet and Coffroth 2004
	Bahamas	<i>Briareum asbestinum</i> , <i>Plexaura flexuosa</i> , <i>Pseudoplexaura</i> spp.	Goulet et al. 2008, LaJeunesse 2002
	Mexico	<i>Gorgonia</i> spp, <i>Pseudopterogorgia</i> spp, <i>Eunicea</i> spp, <i>Pseudoplexaura</i> spp	Goulet et al. 2008, Goulet and Coffroth 2004
	Panama	<i>Pseudopterogorgia</i> spp, <i>Eunicea</i> spp, <i>Pseudoplexaura</i> spp	Goulet et al. 2008, Goulet & Coffroth 2004;
	US Virgin Islands	<i>Pseudoplexaura</i> spp	LaJeunesse et al. 2003
	Florida keys	<i>Gorgonia</i> spp, <i>Leptogorgia</i> sp., <i>Pseudopterogorgia</i> spp	Santos et al. 2003
C <i>Cladocopium</i>	Bermuda	<i>Pseudoplexaura</i> spp	Goulet et al. 2008
	Israel	<i>Cladiella</i> spp, <i>Rhytisma</i> spp, <i>Sinularia</i> spp, <i>Paralemnalia eburnean</i> , <i>Tubipora musica</i> , <i>Heteroxenia fuscescens</i>	Barneah et al. 2004, Goulet et al 2008.
	Australia	<i>Klyxum</i> spp., <i>Lobophyton</i> spp, <i>Sarcophyton</i> spp, <i>Hicksonella expansa</i> , <i>Pinnigorgia flava</i> , <i>Rumphella</i> spp, <i>Heliopora coerulea</i> , <i>Plumigorgia schoboti</i> , <i>Isis</i> spp, <i>Capnella lacerthliensis</i> , <i>Lemnalia</i> spp, <i>Tubipora musica</i> , <i>Paralemnalia digitiformis</i> , <i>Asterospicularia laurae</i> , <i>Cespitularia</i> spp, <i>Efflatounaria</i> sp., <i>Xenia</i> spp.	Goulet et al. 2008, LaJeunesse et al. 2004a, Van Oppen et al. 2005
	Guam	<i>Lobophyton</i> spp, <i>Sinularia</i> spp <i>Asterionella</i> sp., <i>Subergorgia suberosa</i>	Goulet et al. 2008
	Fiji	<i>Sarcophyton</i> spp, <i>Sinularia</i> spp	Goulet et al. 2008
	Japan	<i>Sarcophyton</i> spp, <i>Sinularia</i> spp, <i>Sinularia</i> spp	Lien et al. 2012
	Hawaii	<i>Sarcothelia</i> sp.	Goulet et al. 2008, LaJeunesse et al. 2004b
	Bahamas	<i>Briareum asbestinum</i> , <i>Eunicea</i> spp	Goulet and Coffroth 2004
	Barbados	<i>Erythropodium caribaeorum</i> ; <i>Briareum asbestinum</i>	Santos et al. 2001
	Panama	<i>Eunicea</i> spp, <i>Plexaurella</i> spp	Goulet et al. 2008
	US Virgin Islands	<i>Plexaurella</i> spp	Goulet et al. 2008
	Bermuda	<i>Eunicea</i> spp	Goulet and Coffroth 2004
	Mexico	<i>Eunicea</i> spp	Goulet and Coffroth 2004
D <i>Durusdinium</i>	Israel	<i>Tubipora musica</i>	Goulet et al. 2008
Australia	<i>Clavularia koellikeri</i> , <i>Isis hippuris</i> , <i>Tubipora musica</i> , <i>Sympodium</i> sp.	Van Oppen et al. 2005	
G <i>Gerakladium</i>	Australia	<i>Junceella fragilis</i> , <i>Euplexaura nuttingi</i>	Van Oppen et al. 2005

octocorals *Erythropodium caribaeorum* and *Briareum asbestinum* in Barbados, Bahamas, and other tropical regions (Santos et al. 2001; Goulet and Coffroth 2004). Similarly, the octocoral *Nephthea* spp and *Tubipora musica* of Israel and Australia are observed to harbor four clades such as A, B, C, and D (Goulet et al. 2008) and two clades such as C and D (Van Oppen et al. 2005) respectively (Table 4).

6 *Symbiodinium* association with other species

Endosymbiotic dinoflagellate exhibits symbiotic association with other species as well, such as clams, sponges,

foraminifera, sea anemones, and sea jelly. Sea anemones of northern Persian Gulf islands harbored a greater number of *Symbiodinium* clade C as their habitat is in the intertidal region (Moghaddam et al. 2018). Hence *Symbiodinium* clade C is highly tolerant to environmental conditions like higher water column temperature and direct sunlight exposure during low tide (Moghaddam et al. 2018). Marine sponges belong to the Phylum Porifera. The attractive color of the sponges represents their association with the Symbiodiniaceae family. *Symbiodinium* clade G is harbored by sponges of the Western Pacific and western Atlantic oceans (Ramsby et al. 2017). From the island of Guam, the Micronesia reef region has revealed a high density of *Symbiodinium* clades and subclades in foraminifera species (*Sorites* sp.,

Table 4 Harboring multiple clades in single host (in some Octocorals)-worldwide distribution

Host (octocoral)	Clade	Location	Reference
<i>Cladiella</i> spp	C, D	Australian reefs	LaJeunesse et al. 2004a
<i>Klyxum</i> spp	C, D		Van Oppen et al. 2005
<i>Erythropodium caribaeorum</i>	B, C	Barbados, Bahamas, and other tropical regions	Santos et al. 2001
<i>Briareum asbestinum</i>	B, C		Goulet and Coffroth 2004
<i>Nephthea</i> spp	A, B, C, D	Israel and Australian reefs	Goulet et al. 2008
<i>Nephthea</i> sp.	C1 and B36	Great Barrier Reef (GBR), Australia	Tonk et al. (2014)
<i>Tubipora musica</i>	C, D	Australian reefs	Van Oppen et al. 2005

Amphisorus kudakajimaensis, *A. hemprichii*, and *Marginopora* sp.). *Symbiodinium* clades C, D, F, G, and H are harbored in foraminifera species and many subclades are also associated with that species (Pochon et al. 2007). The study of *Symbiodinium* distribution in giant clams from Indonesia reported clades A, C, and D as widely distributed in giant clams. Where 42% of clams harbored multiple clades in an individual and 15% of clams had harbored various types of sub-clades from a single clade (DeBoer et al. 2012). Also, *Symbiodinium* clade C and D were present in high-level temperature conditions, and clade A was found in low-temperature conditions. Thus, clades C and D could tolerate high temperatures than clade A (DeBoer et al. 2012). Sea jelly is also associated with endosymbiotic algae but their clade distribution is low with the host than the other species. In the presence of *Symbiodinium*, sea jelly tentacles exhibit various color morphs and in their polyp stages, Sea jelly is capable to directly uptake the *Symbiodinium* from the water column. Thereby the sea jelly of the Red sea exclusively harbored *Symbiodinium* clade A1 (Lampert 2016).

7 Discussion

Coral reef ecosystems are biodiversity hotspots of huge economical value and biological diversity, providing habitats to one-third of marine species (Plaisance et al. 2011). These reef-building corals turn up for symbiosis with photosynthetic dinoflagellates (Muscatin and Porter 1977) and these endosymbiont dinoflagellates power up the coral reefs and stony coral growth (LaJeunesse et al. 2018). Corals relationship to dinoflagellates determines the system's response to varied environmental stress, besides the reef growth (deposits of calcium carbonate) (Muscatin and Porter 1977). Their relationship is greatly sensitive to stress such as increased salinity, temperature, nutrients, and solar irradiances that diminish photosynthetic efficiency and augment reactive

oxygen species generation. Which, when not being detoxified by the host ROS (Reactive oxygen species) scavengers and antioxidants, can eventually attribute to coral bleaching events due to their endosymbiont's loss (Ochsenkuhn et al. 2017). Past research had discovered that the coral susceptibility to stress depends on the type of clade they harbor (Rosic and Dove 2011). Varied host and symbiont combinations can provide ecological advantages in different niches, as the symbiont type could influence the coral growth rate (Little et al. 2004) and their potential to get through acute stress (Baker 2001). It is suggested that the prolonged environmental conditions had brought evolutionarily diverse *Symbiodinium* or clade lineages (Rowan and Powers 1991; LaJeunesse 2002). Likely, coral with thermal tolerant symbiont clade D is more resistant to elevated temperatures (Berkelmans and Van Oppen 2006; Desalvo et al. 2010; Reynolds et al. 2008). The adult corals are capable of attaining increased tolerance that results from the change in the dominant *Symbiodinium* clade C to D in their tissues and the level of thermal tolerance gained would be around 1-1.5 °C (Berkelmans and Van Oppen 2006). This Symbiont shuffling is by the already existing type present in coral tissues and not from exogenous environmental uptake (Berkelmans and Van Oppen 2006).

Various investigations had explored the expression of heat shock proteins (Hsp70 and Hsp90) of endosymbiont as a response to thermal stress. HSPs (Heat shock proteins) are molecular chaperones that prevent cellular damage in the circumstances of environmental stress (Rosic et al. 2011). They maintain regular cellular functions such as protein folding, degradation, unfolding, transport, and aggregation (Sorensen et al. 2003), where these conserved proteins carry out cell signaling, cell differentiation, and morphogenesis, cell protection against apoptosis and stress (Beissinger and Buchner 1998; Arya et al. 2007). HSPs are up-regulated during exposure to short-term stress or elevated temperature conditions (Rosic et al. 2011). Compared to the HSPs of coral host, their algal symbiont's HSPs holds potential superior adaptations to thermal stress (Csaszar et al. 2010). In *A. millepora*, a reef-building coral, their *Symbiodinium* genotype is evaluated to influence strongly the coral holobiont fitness by survival, growth, and thermal tolerance (Mieog et al. 2009).

The distribution of coral species is largely correlated based on prevailing temperature and light gradients. Thus, influenced by light tolerance and photosynthetic properties of coral symbionts (host-symbiont specificity) in their biogeographic distribution Iglesias-Prieto et al. 2004; LaJeunesse 2002; LaJeunesse et al. 2003; LaJeunesse et al. 2004) (Fig. 1). Hence predominant clades of the *Symbiodinium* phylotypes such as A, B, C, and D together with their host are observed in characteristic depths (LaJeunesse et al.

2002; Thornhill et al. 2006). Thereupon shallow-water corals are prevalent with Clade A *Symbiodinium* that produces the mycosporine-like amino acids (MAA) (UV protective) in abundance (Fig. 1). While other clades with depth correlation produce hospice amounts of MAA, especially, mycosporine glycine that absorbs UV-B radiations effectively (LaJeunesse et al. 2002; Banaszak et al. 2006). Mycosporine-like amino acids are water-soluble components, composed of cyclohexanone chromophores bound to amino acid residues. They are characterized to possess a maximum absorbance at UVA and UVB ranges (310–362 nm) and hold photoprotective, antioxidant scavenging and suppress singlet oxygen-induced damages (Rosic and Dove 2011; Hoegh-Guldberg and Jones 1999) (Fig. 1). Likely, photoinhibition accelerated due to elevated temperatures, which underlies bleaching in corals. In response to this, *Symbiodinium* of Clade A display improved competencies for alternative photosynthetic electron transport pathways. *Symbiodinium* of Clade A undergoes light-induced antenna complex dissociation from reaction centers of photosystem II, which promotes survival of Clade A associated cnidarians at higher light intensities (Fig. 1). Thereby conferring resistance to bleaching (Reynolds et al. 2008). Similarly, the coral-*Symbiodinium* associations found in the Red Sea and Persian/Arabian gulf represent coral habitats in most saline environments. Investigations of such corals and *Symbiodinium* had revealed that the cells exposed to higher salinity had synthesized higher levels of osmolyte floridoside called osmolyte 2-O-glycerol- α -galactopyranoside, found in both *in vitro* and the host coral animals (Ochsenkuhn et al. 2017). Thereby such coral and *Symbiodinium* cells serve a dual function as a compatible organic osmolyte and a reactive oxygen species scavenger (Ochsenkuhn et al. 2017). Also, coral *Symbiodinium* serves diagnostics through the lipid composition too. The lipid composition of the *Symbiodinium* thylakoid membrane acts as an important determinate of insensitivity to thermal stress. The lipid saturation in the thylakoid membrane reveals a critical threshold temperature that separates the sensitive species of zooxanthellae from the tolerant ones. Thus, lipid composition is a potential diagnostic of the thermally induced bleaching observed in scleractinian corals (Tchernov et al. 2004).

8 Conclusions

Coral reefs are biologically diverse and thus pose huge economical value. Relationship of coral with dinoflagellates gears their productivity. These endosymbionts are classified into several clades that serve a major role in coral sustenance under adverse conditions. They exhibit different stages of tolerance to stress. For example, *Symbiodinium* clades C

and D that are present in a high level of temperature conditions were identified and recognized as temperature tolerant clades. At critical conditions, the corals are observed to change their subclades from stress-sensitive subclades to stress-tolerant subclades. Clade A of *Symbiodinium* had displayed UV protection at instances of high irradiances and some other clades are found to be osmotolerant, gained through adaptation in higher saline environmental conditions. Hence an intricate observation into the coral symbiont relationship and the implementation of *in vitro* transmission studies of stress-tolerant clades into coral hosts would serve beneficial to achieving coral resilience under various stress conditions.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest or competing interests.

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