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Symbiodiniaceae Diversity in Red Sea Coral Reefs & Coral Bleaching

Maren Ziegler, Chatchanit Arif, and Christian R. Voolstra

Abstract

This chapter introduces Symbiodiniaceae, the diverse group of dinoflagellate microalgae, that form an obligate symbiosis with corals and other coral reef organisms. The Symbiodiniaceae cells reside within the coral tissue, their photosynthesis fuels the productivity and diversity of coral reef ecosystem, and the breakdown of this symbiosis leads to coral bleaching and may entail the death of the host. Here, we summarize Symbiodiniaceae taxonomy and phylogeny and the molecular tools that are used to study Symbiodiniaceae diversity in the Red Sea. We provide an overview over all described Symbiodiniaceae species and discuss the functional diversity within this phylogenetically diverse group as well as the implications of this diversity for coral-Symbiodiniaceae pairings and ecological niche partitioning in coral reef ecosystems. We review host-Symbiodiniaceae associations of 57 host genera in the Red Sea and discuss the emerging patterns in light of their wider biogeographic distribution. Last, we summarize how climate change-induced thermal anomalies have repeatedly led to coral bleaching and mortality in the Red Sea and how they threaten these reef ecosystems, otherwise thought to be comparatively resilient. We conclude with a perspective of important topics for Symbiodiniaceae research in the Red Sea that have the potential to contribute to a broader understanding of the basis of thermotolerance in this fragile symbiosis.

Keywords

Symbiodiniaceae diversity · Biogeography · Host-symbiont association · Symbiosis · Molecular tools · ITS2 · Coral bleaching

5.1 Introduction

Coral reefs harbor the largest biodiversity of all marine ecosystems (Connell 1978; Roberts et al. 2002). Scleractinian or hermatypic, reef-forming, corals are primarily adapted to live in the light-flooded zone of warm tropical and subtropical oceans (Kleypas et al. 1999). Despite the oligotrophic conditions prevalent in these waters, coral reefs belong to the most productive ecosystems (Connell 1978; Patton et al. 1977; Roberts et al. 2002). The key to the success of hermatypic corals is the association with autotrophic dinoflagellates of the family Symbiodiniaceae in an obligate symbiosis (Muscatine and Porter 1977). More generally, a great variety of coral reef invertebrate taxa has been found to host Symbiodiniaceae symbionts, such as soft corals (Octocorallia) (Barneah et al. 2004; Benayahu et al. 1989; Goulet and Coffroth 2003), sponges (Porifera) (Carlos et al. 1999; Vicente 1990), flat worms (Plathyelminthes) (Barneah et al. 2007), soritid Foraminifera (Leutenegger 1984; Müller-Merz and Lee 1976; Pochon et al. 2010), and molluscs (Mollusca) such as nudibranchs and tridacnid giant clams (Belda-Baillie et al. 1999; Burghardt et al. 2005; Jeffrey and Haxo 1968; Taylor 1968; Ziegler et al. 2014a).

The Symbiodiniaceae cells are located in the endodermal tissue of their coral hosts where they are found in membrane-bound modified lysosomes, the symbiosomes (Fig. 5.1; Trench 1979; Wakefield and Kempf 2001). The spatial proximity of this endosymbiotic association facilitates a system

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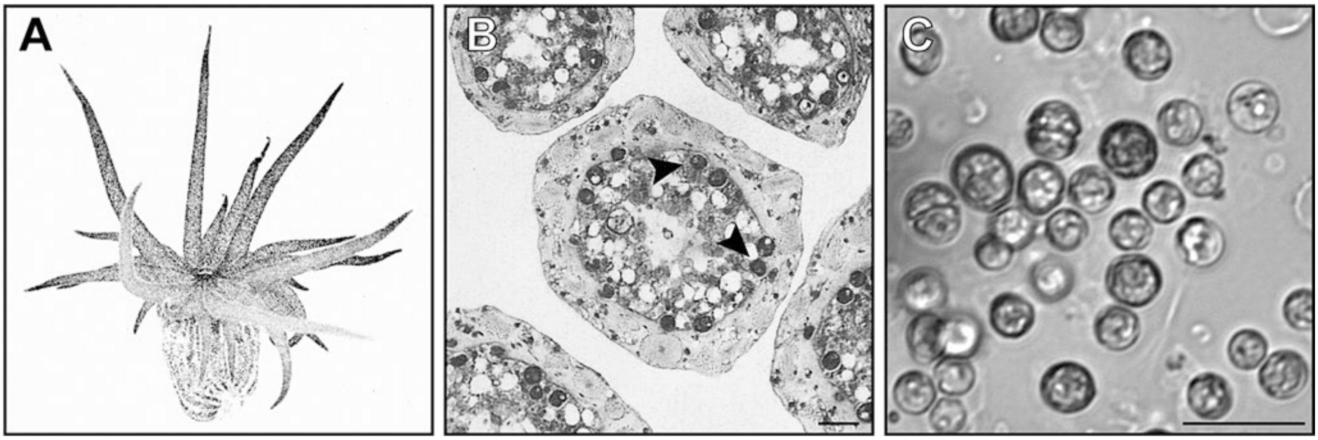

Fig. 5.1 **Symbiodiniaceae cells are abundant in endodermal tissues of Cnidarians**. (**A**) Fluorescence image of the Cnidarian model organism Aiptasia (strain CC7); Symbiodiniaceae cells are visualized through chlorophyll fluorescence in dark grey/black, whereas the anemone's body is translucent; (**B**) stained tissue cross-section of polyps of the soft coral *Bayerxenia* with Symbiodiniaceae cells (arrowheads) located in the endodermal tissue, which borders the cell-free mesogloea and is surrounded by ectodermal tissue; (**C**) Symbiodiniaceae cells of strain SSB01 (genus *Breviolum*, ITS2 type **B1**) in culture. Scale bars = 20 μm. Photocredit: (**A** & **C**) Fabia Simona, KAUST, (**B**) Maren Ziegler, KAUST

of tight recycling of nutrients and metabolic products (Muscatine and Porter 1977; Rädecker et al. 2015; Tanaka et al. 2006; Trench 1979). The Symbiodiniaceae cells receive protection from damaging ultraviolet radiation (UVR) (Banaszak and Trench 1995a, 1995b) and are provided with carbon dioxide (CO_2) from the coral host, which they utilize for their highly efficient photosynthesis (Falkowski et al. 1984; Muscatine and Porter 1977; Muscatine et al. 1989). The photosynthates in turn, are passed on to the coral host, typically as compounds of low-molecular weight such as glucose, glycerol, and amino acids (Burriesci et al. 2012; Markell and Trench 1993; Trench 1993). In a healthy coral, photosynthesis can cover almost the entire energy demand of the coral host (Muscatine 1990; Muscatine et al. 1984; Muscatine and Porter 1977). Supported by high photosynthetic production rates of their endosymbionts, corals secrete calcium carbonate skeletons that give rise to the large three-dimensional coral reef structures that in turn provide the habitat complexity to support a large diversity of species (Kawaguti and Sakumoto 1948; Pearse and Muscatine 1971).

The Red Sea represents a unique and rather extreme environment with thriving coral reef landscapes. Because of its long-term thermal regime at the upper limits of coral reef occurrence, it represents a suitable location to explore the perspectives of host-Symbiodiniaceae associations under climate change and to study their adaptation and acclimatization mechanisms (Hume et al. 2016). Caused by long geographic isolation and repeated extinction events, Red Sea coral reef communities are characterized by a larger proportion of endemic species than previously assumed (DiBattista et al. 2013); amongst them many Symbiodiniaceae-bearing host taxa, including e.g., octocorals (Fabricius and Alderslade 2001), scleractinian corals (Terraneo et al. 2014; Veron et al. 2015), and tridacnid clams (Richter et al. 2008). The evolutionary trajectories of these host species affect the rates and patterns of diversification of the associated symbionts (Thornhill et al. 2014), but comprehensive data on the evolutionary history of the host-Symbiodiniaceae system in the Red Sea is wanting.

5.2 Symbiodiniaceae Taxonomy and Phylogeny– Challenges in Diversity Analyses

The term 'zooxanthellae' (Brandt 1881) is commonly used to refer to dinoflagellate endosymbionts of the family Symbiodiniaceae in the order Suessiales (LaJeunesse et al. 2018). However, this term originally includes any golden-brown ('xanthos') algae of diatom and dinoflagellate origin living in symbioses with animals ('zoo') (Blank and Trench 1985, 1986; Trench 1979). The family Symbiodiniaceae (Fensome et al. 1993) was recently revised including a formal description of 7 genera (i.e. *Symbiodinium*, formerly clade A; *Breviolum*, formerly clade B; *Cladocopium*, formerly clade C; *Durusdinium*, formerly clade D; *Effrenium*, formerly clade E; *Fugacium*, formerly clade F; *Gerakladium*, formerly clade G) and the identification of further 8 lineages that require taxonomic classification (LaJeunesse et al. 2018). *Symbiodinium microadriaticum* LaJeunesse 2017 was the first Symbiodiniaceae species to be formally described by Freudenthal (1962). This original description was later found to be invalid because of the lack of a holotype that was only designated in 2017 (LaJeunesse 2017). *S. microadriaticum* was isolated from the scyphozoid upside-down jellyfish *Cassiopea xamachana* Bigelow, 1982 in the Bahamas by

McLaughlin and Zahl (1957, 1959) and by David A. Schoenberg from the same host in Florida in 1977 (LaJeunesse 2017). Because the first isolate of the species was lost, the second isolate, also known under culture strain number CCMP 2462/rt-061, was used to designate a species holotype (LaJeunesse 2017); the genome sequence of this species (strain CCMP2467) became recently available (Aranda et al. 2016). Since the original description, *S. microadriacticum* has been encountered in a range of hosts throughout the Red Sea (LaJeunesse 2001; Sawall et al. 2014; Ziegler et al. 2014b), as well as in other oceans (Correa and Baker 2009; LaJeunesse 2002; Reimer et al. 2007; Stat and Gates 2008; Stat et al. 2009).

Initially, taxonomic studies on these microalgae were hampered by the lack of distinguishing morphological attributes in symbiosis and further aggravated by the difficulty to maintain them in culture (Freudenthal 1962; Taylor 1969). Until today, only members of *Cladocopium* can be morphologically diagnosed and distinguished from other genera in the family Symbiodiniaceae (LaJeunesse et al. 2018). Consequently, *S. microadriaticum* was at first perceived as the exclusive panmictic symbiotic dinoflagellate species in cnidarians (Kevin et al. 1969; Taylor 1968, 1969), until studies on morphology, physiology, and biochemistry of cultured isolates revealed distinct ecological features and led to the description of several novel species in the family Symbiodiniaceae (Table 5.1; Banaszak et al. 1993; Blank and Trench 1985; Chang et al. 1983; Schoenberg and Trench 1980a, 1980b, 1980c; Trench and Blank 1987).

Until today, the establishment of cultures of different Symbiodiniaceae species remains a challenge (Krueger and Gates 2012; Santos et al. 2001). Hence, the advancement of Symbiodiniaceae taxonomy and phylogeny was driven by molecular techniques. Sequence analyses of the ribosomal small subunit (SSU) 18S rDNA revealed high phylogenetic divergence between Symbiodiniaceae lineages up to that between taxonomic orders of non-symbiotic dinoflagellates (Rowan and Powers 1992). The investigation of additional DNA marker regions, such as the ribosomal large subunit (LSU) 28S rDNA together with 18S rDNA from a wide array of invertebrate hosts corroborated these findings and prompted the division into 9 phylogenetic clades, designated A to I (Coffroth and Santos 2005; Loh et al. 2001; Pochon and Gates 2010; Pochon et al. 2004; Rodriguez-Lanetty et al. 2001; Rowan 1998; Stat et al. 2006), and later, a further subdivision into 15 genus-level lineages (LaJeunesse et al. 2018). But not all Symbiodiniaceae species are specific in their association with scleractinian corals. For example, to date members belonging to clades H and I have only been encountered in association with benthic Foraminifera (Pochon and Gates 2010; Pochon and Pawlowski 2006; Pochon et al. 2001), while scleractinian corals most commonly associate with Symbiodiniaceae of the genera *Symbiodinium*, *Breviolum*, *Cladocopium*, *Durusdinium* (formerly clade A to D), and occasionally with the genera *Fugacium* and *Gerakladium* (formerly clade F lineage Fr5 and clade G) as well as the undescribed genus represented by clade F lineage Fr2 (Baker 2003; Coffroth and Santos 2005; Rowan 1998).

The distinction into evolutionary subgeneric lineages has received further support from sequence analyses of the chloroplast LSU 23S (Santos et al. 2002) and the mitochondrial cytochrome c oxidase subunit 1 (COI) markers (Stern et al. 2010; Takabayashi et al. 2004). However, these investigations have also underlined limitations of such coarse taxonomic approaches, highlighting the importance of addressing discrete evolutionary units (i.e., species) at higher resolution. Analyses using the fast-evolving, non-coding internal transcribed spacer (ITS) regions of rDNA promised to fill this gap and drove the sub-division into so called phylotypes (hereafter referred to as 'types'), designated by the clade followed by an alphanumeric identifier (e.g., A1, C1, C2, etc.; Baillie et al. 2000; LaJeunesse 2001; van Oppen et al. 2001). Until today, hundreds of different (ITS2) Symbiodiniaceae types have been discovered, but to date only 25 of them have formally been described as biological species (Table 5.1). While evidence attests reasonable validity to the ITS2 marker for estimating Symbiodiniaceae species diversity in the majority of cases (Sampayo et al. 2009; Thornhill et al. 2007), recent research efforts have been aimed at developing more specific ITS2 primer pairs (Hume et al. 2018b) and a novel analytical framework (http://symportal.org; Hume et al. 2019) to delineate Symbiodiniaceae species diversity. In addition, combinations of alternative molecular markers including genes from all 3 compartments, i.e., chloroplast (cp23S, psbA), mitochondrion (COI, cob), and nucleus (nr28S, elf2), as well as microsatellites, are being analyzed to resolve species relationships (Lajeunesse et al. 2012; LaJeunesse and Thornhill 2011; LaJeunesse et al. 2014; Pochon et al. 2012, 2014).

Overall, the most commonly used method for determination of Symbiodiniaceae types has been denaturing gradient gel electrophoresis (DGGE) of polymerase chain reaction (PCR) amplified ITS2 sequences, and approximately half (46%) of all studies conducted in the Red Sea used this technique. A side effect of DGGE analyses on multicopy loci harboring intragenomic variation, such as ITS2, is the occurrence of heteroduplexes, which are mismatched DNA strands from different ITS2 copies within a sample. Although this is sometimes seen as a disadvantage of DGGE ITS2 analyses, heteroduplexes have successfully been used as a diagnostic feature that can increase DGGE resolution (Myers et al. 1985). One further constraint of the DGGE technique is that the detection limit of different Symbiodiniaceae types within mixed samples varies between clades and commonly ranges between 1 to 10%, which results in an underestimation of the total diver-

Table 5.1 List of formally described genera and species belonging to the family Symbiodiniaceae and "*nomina nuda*" (published specific epithets without formal diagnosis)

Symbiodiniaceae genera and species	Authors[a]	References	Isolated from	clade	ITS2 type[b]	Region	Country / type locality
Symbiodinium	Gert Hansen & Daugbjerg	Hansen and Daugbjerg (2009)					
S. microadriaticum	LaJeunesse	Freudenthal (1962), Trench and Blank (1987), Blank and Huss (1989), Kevin et al. (1969), LaJeunesse (2017), Lee et al. (2015), and Loeblich and Sherley (1979)	*Cassiopea xamachana*	A	A1	Caribbean	Florida Keys
"*S. cariborum*"			*Condylactis gigantea*	A	A.1.1	Caribbean	Jamaica
"*S. microadriacticum var. condylactis*"			*C. xamachana /Cassiopea frondosa*	A	A.1.1	Caribbean	Florida Keys/Jamaica
S. pilosum	Trench & Blank	Trench (2000) and Trench and Blank (1987)	*Zoanthus sociatus*	A	A2	Caribbean	Jamaica
"*S. corculorum*"			*Corculum cardissa*	A	A2	West Pacific	Palau
"*S. meandrinae*"			*Meandrina meandrites*	A	A2	Caribbean	Jamaica
"*S. corculorum*"			*Corculum cardissa*	A			
S. natans[d]	Hansen & Daugbjerg	Hansen and Daugbjerg (2009)	free-living, planktonic	A	A3	Northeast Atlantic	Canary Islands
"*S. fitti*"			*Acropora palmata, Tridacna maxima*	A	A3	Caribbean/Indopacific	
S. tridacnidorum	Lee, Jeong, Kang & LaJeunesse	Lee et al. (2015)	*Hippopus hippopus, Tridacna gigas*	A	A3	Indopacific	Great Barrier Reef, Palau
S. linucheae	(Trench and Thinh) LaJeunesse	LaJeunesse (2017) and Trench and Thinh (1995)	*Linuche unguiculata*	A	A4	Western Atlantic	Bermuda
S. necroappetens	LaJeunesse, Lee, Knowlton & Jeong	LaJeunesse et al. (2015)	*Orbicella annularis*	A	A13 (A1.1)	Caribbean	Jamaica
Breviolum	J.E.Parkinson & LaJeunesse	LaJeunesse et al. (2018)					
B. minutum[d]	(LaJeunesse, Parkinson & Reimer) J.E.Parkinson & LaJeunesse	LaJeunesse et al. (2012)	*Aiptasia sp.*	B	B1	Caribbean	Florida Keys
B. antillogorgium	(Parkinson, Coffroth & LaJeunesse) J.E.Parkinson & LaJeunesse	Parkinson et al. (2015)	*Antillogorgia bipinnata*	B	B1	Caribbean	Florida Keys
B. pseudominutum	(Parkinson, Coffroth & LaJeunesse) J.E.Parkinson & LaJeunesse	Parkinson et al. (2015)	*Oculina diffusa*	B	B1	Western Atlantic	Bermuda
"*B. pulchrorum*"			*Aiptasia pulchella*	B	B1	Central Pacific	Hawaii
"*B. bermudense*"			*Aiptasia tagetes*	B	B1	Western Atlantic	Bermuda
B. dendrogyrum	A.M. Lewis, A.N. Chan & LaJeunesse	Lewis et al. (2018)	*Dendrogyra cylindrus*	B	B1-1k	Caribbean	Curacao
B. faviinorum	A.M. Lewis & LaJeunesse	Lewis et al. (2018)	*Diploria labyrinthiformis* and other Faviidae, and the genera *Isophyllia* and *Orbicella*	B	B1-14-14a-24	Caribbean	Curacao

B. meandrinium	A.M. Lewis & LaJeunesse	Lewis et al. (2018)	*Meandrina meandrites* and other Meansdrinidae and the genus *Orbicella*	B	B1-20	Caribbean	Curacao
B. psygmophilum	(LaJeunesse, Parkinson & Reimer) J.E.Parkinson & LaJeunesse	Lajeunesse et al. (2012)	*Oculina diffusa*	B	B2	Western Atlantic	Bermuda
"B. muscatinei"			*Anthopleura elegantissima*	B	B4	East Pacific	USA
B. endomadracis	(Parkinson, Coffroth & LaJeunesse) J.E.Parkinson & LaJeunesse	Parkinson et al. (2015)	*Madracis spp.*	B	B7	Caribbean	Curacao
B. aenigmaticum	(Parkinson, Coffroth & LaJeunesse) J.E.Parkinson & LaJeunesse	Parkinson et al. (2015)	*Porites astreoides*	B	close to B23	Caribbean	Florida Keys
Cladocopium	LaJeunesse & H.J. Jeong	LaJeunesse et al. (2018)					
C. goreaui[d]	LaJeunesse & H.J. Jeong	LaJeunesse et al. (2018), Trench (2000), and Trench and Blank (1987)	*Heteractis/Rhodactis lucida*	C	C1	Caribbean	Jamaica
C. thermophilum	(Hume, D'Angelo, Smith, Stevens, Burt & Wiedenmann) LaJeunesse & H.J. Jeong	Hume et al. (2015), and Hume et al. (2018a)	*Porites lobata*	C	C3, C3gulf[c]	Persian Gulf	United Arab Emirates, Abu Dhabi
Durusdinium	LaJeunesse	LaJeunesse et al. (2018)					
D. glynnii	(Wham & LaJeunesse) LaJeunesse	Wham et al. (2017)	*Pocillopora type I, Seriatopora, Montipora*	D	D1, D1-4-6	Entire Pacific	Palau
D. trenchii[d]	(LaJeunesse) LaJeunesse	LaJeunesse et al. (2014)	various Scleractinia	D	D1-4 (D1a)	West Pacific	Japan
D. eurythalpos	(LaJeunesse & Chen) LaJeunesse	LaJeunesse et al. (2014)	*Oulastrea crispata*	D	D8, D8-12, D12-13, D13	West Pacific	Taiwan
D. boreum	(LaJeunesse & Chen) LaJeunesse	LaJeunesse et al. (2014)	*Oulastrea crispata*	D	D15	West Pacific	Taiwan
Effrenium	LaJeunesse & H.J. Jeong	LaJeunesse et al. (2018)					
S. voratum[d]	(Jeong, Lee, Kang & LaJeunesse) LaJeunesse & H.J. Jeong	Jeong et al. (2014)	free-living to symbiotic	E		Pacific Ocean / Mediterranean	Korea
"S. californium"			*Anthopleura elegantissima*	E	E1	Central Pacific	Hawaii
Fugacium	LaJeunesse	LaJeunesse et al. (2018)					
F. kawagutii[d]	LaJeunesse	LaJeunesse et al. (2018),Trench (2000), and Trench and Blank (1987)	*Montipora verrucosa*	F	F1	Central Pacific	Hawaii
Gerakladium	LaJeunesse	LaJeunesse et al. (2018)					
G. endoclionum[d]	(Ramsby & LaJeunesse) LaJeunesse	Ramsby et al. (2017)	*Cliona orientalis*	G		Indopacific	Great Barrier Reef
G. spongiolum	(M.S. Hill & LaJeunesse) LaJeunesse	Ramsby et al. (2017)	*Cliona varians*	G		Caribbean	Florida Keys

[a] For species of newly erected genera, the original species authors are given in parentheses and the author of the new genus is given at the end in accordance with taxonomic nomenclature

[b] Please note that different species of Symbiodiniaceae may have an identical main ITS2 sequence. Former designated ITS2 types are listed in parentheses.

[c] Minor sequence variant not resolved by DGGE.

[d] Type species of the genus

sity (LaJeunesse et al. 2008; Thornhill et al. 2006b). Bacterial cloning, on the other hand, which was used in about one fifth (21%) of Red Sea studies, overestimates the diversity, because it retrieves a high number of intragenomic ITS2 variants, alongside the intergenomic variability within a sample (Arif et al. 2014; Thornhill et al. 2007). The remaining third (29%) of studies from the Red Sea used restriction fragment length polymorphisms (RFLPs) of 18S rDNA, which was used in Symbiodiniaceae molecular research early on (Rowan and Powers 1991a, 1991b). So far, only one study (corresponding to 4%) used high-resolution, high-throughput next-generation sequencing (NGS), yielding a high number of ITS2 sequence reads, thus capturing a high proportion of the diversity in mixed Symbiodiniaceae assemblages and providing information on the relative abundance of distinct sequence variants within a sample (Ziegler et al. 2017).

5.3 Functional Diversity of Different Host-Symbiodiniaceae Pairings

Symbiodiniaceae species can be attributed specific physiological and biochemical properties, which reflect their adaptation to distinct environments. These adaptations translate into different properties for the associated coral host, for example by increasing growth rates in coral recruits depending on the Symbiodiniaceae type (Little et al. 2004). Consequently, the ability to associate with different Symbiodiniaceae types is an important factor influencing a coral species' distribution range (Rodriguez-Lanetty et al. 2001), metabolic performance (Cooper et al. 2011b), and stress tolerance (Abrego et al. 2008; Berkelmans and van Oppen 2006; Howells et al. 2012).

Between coral species, the niche partitioning in host-Symbiodiniaceae associations is most commonly observed along depth-mediated gradients of light and temperature, where it is an important variable explaining depth zonation. For example, photosynthetic properties of *Durusdinium* type D1 symbionts in *Pocillopora verrucosa* Ellis & Solander, 1786 dominating shallow habitats between 0 – 6 m were distinct from those of *Cladocopium* type C1c in *Pavona gigantea* Verrill, 1869, occurring in deeper water from 6 – 14 m (Iglesias-Prieto et al. 2004). These host-specific symbionts were adapted to different light regimes, and host-symbiont fidelity contributed to vertical niche partitioning between the 2 coral species (Iglesias-Prieto et al. 2004). Observations of four scleractinian genera over a large depth gradient in the central Red Sea (Ziegler et al. 2015a) and within the genus *Agaricia* in the Caribbean (Bongaerts et al. 2013) support the concept of host-specific Symbiodiniaceae association as one of the drivers of depth-niche partitioning between taxa.

A possible determinant of host-symbiont specificity is the mode of symbiont acquisition. In brooding and some broadcast spawning corals, Symbiodiniaceae cells are directly passed on to the offspring vertically (Trench 1987). In contrast, corals with horizontal symbiont transmission have symbiont-free gametes and each generation has to acquire symbionts from the environment *de novo* (Trench 1987). While vertical symbiont transmission avoids the risk associated with having to find new symbiont partners, as is the case with horizontal transmission, the resulting tight co-evolution may also limit the flexibility of the host to associate with a wide (phylogenetic) range of symbionts. In fact, vertical symbiont transmission promotes the evolution of specialist symbionts (LaJeunesse et al. 2004a). In contrast, each generation in horizontally transmitting coral species can potentially yield new host-symbiont combinations and the initial uptake of Symbiodiniaceae is relatively flexible (Abrego et al. 2009; Coffroth et al. 2001; Gómez-Cabrera et al. 2008; Little et al. 2004; Voolstra et al. 2009), although it may be limited by the symbionts' cell size (Biquand et al. 2017). Such flexibility may be particularly important with regard to range expansions (Grupstra et al. 2017) and global climate change (Decelle et al. 2018). However, studies addressing the connection between different reproductive strategies and host-symbiont specificity remain inconclusive, and hence, the issue remains a matter of debate (Barneah et al. 2004; LaJeunesse et al. 2004a, 2004b; Rodriguez-Lanetty et al. 2004; Stat et al. 2008; Thornhill et al. 2006a; van Oppen 2004).

Symbiont generalist coral species are characterized by more flexible Symbiodiniaceae associations (Baker 2003). In these generalist corals, the distribution of Symbiodiniaceae can vary with irradiance levels within a single colony, and in fact most of these coral colonies harbor more than one Symbiodiniaceae genus and/or type at the same time, often in uneven proportions (Mieog et al. 2007; Silverstein et al. 2012). This was first observed in *Orbicella annularis* Ellis & Solander, 1786 and *Orbicella faveolata* Ellis & Solander, 1786, that harbored members of the genera *Symbiodinium* and *Breviolum* in sun-exposed and *Cladocopium* in shaded parts of the colonies (Rowan et al. 1997). Similar patterns were later found in other coral species (Ulstrup and Van Oppen 2003). However, spatial differences in association within a single coral colony do not seem to be a universal phenomenon, as e.g. within colonies of *Pocillopora* symbiont types are distributed uniformly (LaJeunesse et al. 2008; Pettay et al. 2011). More generally, it is assumed that in the majority of cases only a single Symbiodiniaceae taxon is predominant in an individual coral (Goulet and Coffroth 2003; Thornhill et al. 2009; Pettay et al. 2011; Baums et al. 2014).

Stratification of symbionts within generalist species also exists between colonies along environmental gradients. For example, some corals from the genera *Madracis* (Frade et al. 2008) and *Orbicella* (Rowan and Knowlton 1995) associate with different Symbiodiniaceae in shallow and deep water. In the Red Sea, it was recently demonstrated for *Porites lutea* that the symbiont community of a single coral host species is variable across depth, cross-shelf location, and sampling times (Ziegler et al. 2015b). These finding contradict the concept of high symbiont specificity in *Porites* (Ziegler et al. 2015b) and highlight the need for more comprehensive sampling efforts to study the diversity of host-Symbiodiniaceae associations, in particular because this relationship is directly compromised by the consequences of global climate change.

5.4 Symbiodiniaceae Diversity in the Red Sea

Overall, 24 studies reported host-Symbiodiniaceae associations in the Red Sea, spanning 57 host genera belonging to 23 families and 8 orders that were associated with a total of 65 Symbiodiniaceae types from 5 genera (*Symbiodinium*, formerly clade A; *Breviolum*, formerly clade B; *Cladocopium*, formerly clade C; *Durusdinium*, formerly clade D; *Fugacium*, formerly clade F / lineage Fr5; and representatives of clade F lineages Fr2 and Fr4 with yet undescribed genera). Members of the genus *Cladocopium* dominated the endosymbiont assemblages throughout the Red Sea (Fig. 5.2). The majority of host genera (49/57, 86%) were associated with members of *Cladocopium* at least once and a total of 45 *Cladocopium* ITS2 types were recorded (Table 5.2).

The most common ITS2 types were C1 and C41, present in 23 and 21 genera across all Red Sea regions, respectively. In contrast, other *Cladocopium* types displayed more specific associations with their host organisms. For example, although considered a generalist type, *Cladocopium* C3 was found in only 4 genera (*Montipora, Pachyseris, Pocillopora*, and *Xenia*), and C38 was limited to *Montipora*, C161 and C162 to *Stylophora*, C163 to *Seriatopora*, C39 to Agaricidae (*Gardineroseris*, *Leptoseris*, *Pachyseris*, *Pavona*), and C65 to Alcyoniidae (*Lobophytum*, *Sarcophyton*, *Sinularia*) (Table 5.2).

The genus *Symbiodinium* (formerly clade A) was found in 14 host genera, and it occurred in almost even proportions along the Red Sea coast (Fig. 5.2). The overall third most abundant type after *Cladocopium* C1 and C41 was *Symbiodinium* A1, but its occurrence was limited to the genus *Montipora* and the family Pocilloporidae (*Pocillopora*, *Seriatopora,* and *Stylophora*), whose members belonged to the most frequently sampled taxa.

The proportion of host genera found to harbor the genus *Durusdinium* (formerly clade D) increased from 2 (6% of sampled genera) in the north, 9 (30%) in the central north, 16 (57%) in the central Red Sea to 18 and 3 (each representing 75% of sampled genera) in the central south and the southern Red Sea, respectively. More specifically, the genera *Acropora*, *Astreopora*, *Diploastrea*, *Gardineroseris*, *Pavona*, *Pocillopora*, and *Porites* changed from Symbiodiniaceae assemblages consisting of the genera *Symbiodinium* and/or *Cladocopium* to (additionally) containing *Durusdinium* towards the southern localities of their respective distributions (Table 5.2). Other genera, such as *Echinopora*, *Montipora*, and *Stylophora* were found to associate with *Durusdinium* at some localities throughout their range.

The genus *Fugacium* (formerly clade F / lineage Fr5) was found in association with the foraminiferan genus *Amphisorus* in the northern Red Sea. The clade F lineage Fr4 was found in association with the foraminiferan genus *Sorites* in the northern Red Sea, and the clade F lineage Fr2 was found in association with both Foraminifera in the northern and with the coral *Stylophora* in the central Red Sea. The genus *Breviolum* (formerly clade B), uncommon to the Indopacific region, was recorded once in association with *P. verrucosa* (Ziegler et al. 2014b).

5.5 Biogeographic Patterns in Symbiodiniaceae Diversity and Host-Symbiont Associations

The presence of 65 Symbiodiniaceae types encountered in 57 host genera compares favorably with diversity estimates from surveys in other locations. For instance, LaJeunesse et al. (2004b, 2010) sampled a comparable, mixed host assemblage consisting of 58 genera in the Andaman Sea (Thailand) and observed only 37 Symbiodiniaceae types. Similarly, 50 host genera in the Caribbean contained 35 Symbiodiniaceae types (LaJeunesse et al. 2003) and higher numbers of host genera sampled in the Western Indian Ocean (70) and the central Great Barrier Reef (GBR) (72) yielded 47 and 33 Symbiodiniaceae types, respectively (LaJeunesse et al. 2004b, 2010), highlighting the high relative diversity of Symbiodiniaceae in the Red Sea.

The distribution and occurrence of Symbiodiniaceae from the different genera and lineages varies across biogeographic regions. In the IndoPacific, the two main Symbiodiniaceae genera associated with hard corals are *Cladocopium* and *Durusdinium*. Hard coral-symbiont assemblages in the Red Sea share the dominance of *Cladocopium* and the occurrence of *Durusdinium* with those in the IndoPacific, however, they are distinct with regard to the presence of *Symbiodinium* symbionts in Pocilloporidae and few other species. The genus *Symbiodinium* is rarely found in hard corals of the IndoPacific region, while it is common in the Atlantic Ocean. The presence and large diversity of the genus *Breviolum* in the Caribbean and North Atlantic in turn separates these Symbiodiniaceae assemblages from those in the Red Sea. In the Caribbean, *Breviolum*, *Cladocopium*, *Symbiodinium*, and *Durusdinium*, in descending order of prevalence, dominate Symbiodiniaceae assemblages in hard corals, which are considered to be more diverse in relation to the number of

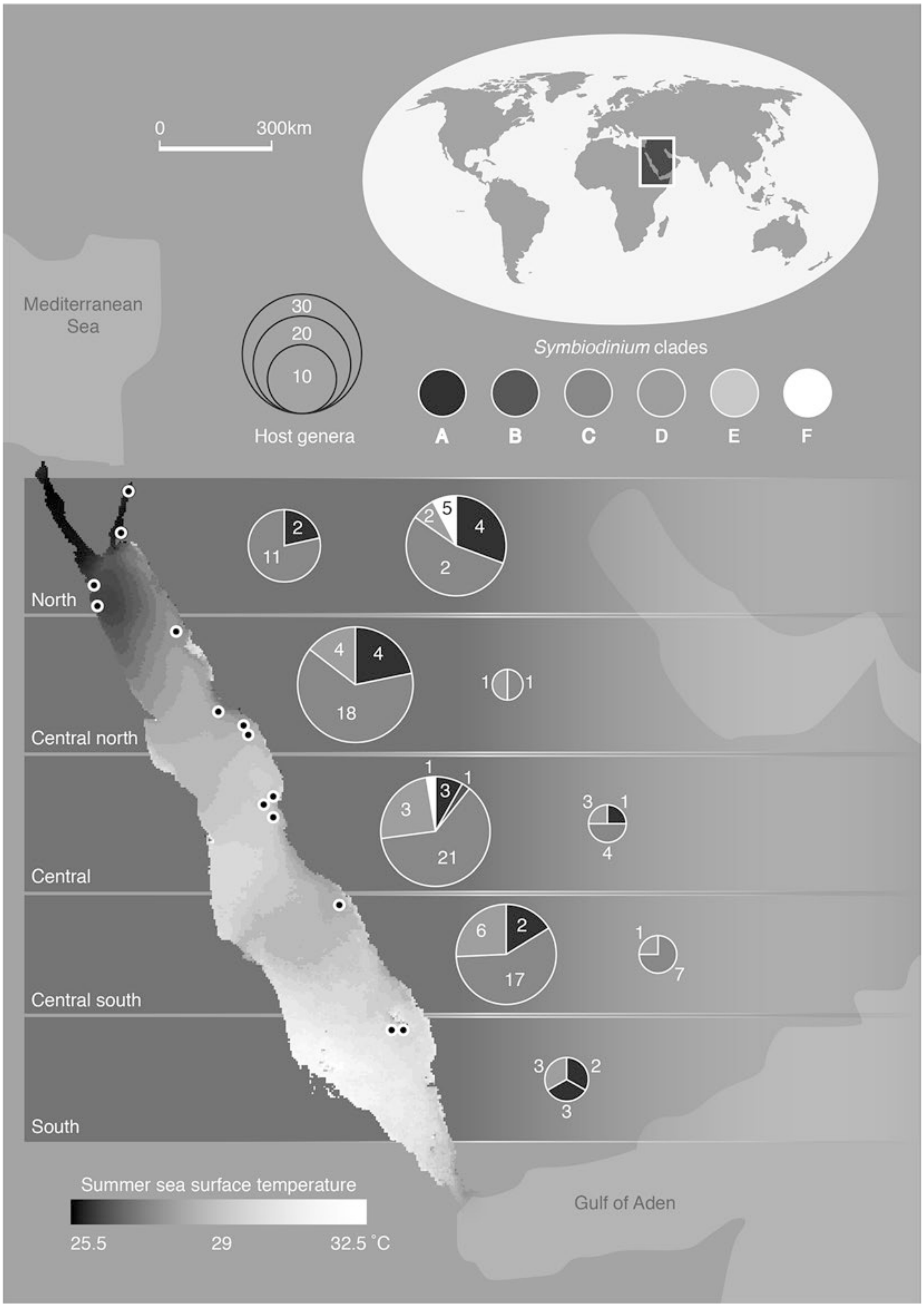

Fig. 5.2 **Distribution of Symbiodiniaceae lineages (formerly clades) in scleractinian corals (left pie charts) and other host organisms (right pie charts) sampled along the coast of the Red Sea.** Symbiodiniacean clades correspond to the recently described genera: former clade A, *Symbiodinium*; former clade B, *Breviolum*; former clade C, *Cladocopium*; former clade D, *Durusdinium*; former clade F lineage Fr5, *Fugacium*; and representatives of clade F lineages Fr2 and Fr4 with yet undescribed genera. Average summer sea surface temperatures are depicted for the Red Sea basin (2004–2013) and sampling sites are demarcated by black circles. Scale bar denotes distances across the Red Sea. Sizes of pie charts denote the number of host genera sampled in each region of the Red Sea (north, central north, central, central south, and south, respectively) and the numbers in the pie charts represent the number of ITS2 phylotypes encountered per clade at a location. (Data based on references listed in Table 5.2)

Table 5.2 **Invertebrate host genera found in association with Symbiodiniaceae ITS2 types along the coast of five Red Sea regions** (N = north, CN = central north, C = central, CS = central south, S = south)

	Genus	Red Sea regions (underlined) and Symbiodiniaceae ITS2 types [a]	References
Scleractinia	*Acanthastrea*	CN: C1, C41	Ziegler et al. (2017)
	Acropora	N: A, C41, C74; CN: A, C, C1, C41; C: C1, C41, D1, D17, D1-4; CS: C1, C41, C41a; S: C41a, D1-4	Baker et al. (2005), Baker et al. (2004), Barneah et al. (2004), Jessen et al. (2013), Pochon et al. (2006), Santos and LaJeunesse (2006), and Ziegler et al. (2017)
	Astreopora	CN: A, C, C41; C: C1, D1; CS: C41, D1, D1-4	Baker et al. (2005) and Ziegler et al. (2017)
	Cladocora	CS: D1–4, D5	Ziegler et al. (2017)
	Coscinarea	C: C1	Ziegler et al. (2017)
	Cyphastrea	CN: C, C1, C1b, C41; CS: C1, C41	Ziegler et al. (2017)
	Diploastrea	CN: C; C: C41, D1, D1–4; CS: D1, D6, D10	Baker et al. (2005), Baker et al. (2004), and Ziegler et al. (2017)
	Echinophyllia	CS: A1, C22	Ziegler et al. (2017)
	Echinopora	CN: C, C1, C41, D; C: D1, D1-4; CS: C1, C41	Baker et al. (2005) and Ziegler et al. (2017)
	Favia	N: C; CN: C, C1, C41; CS: C1, C1b, C41	Baker et al. (2005), Baker et al. (2004), Karako-Lampert et al. (2004), and Ziegler et al. (2017)
	Favites	CN: C; C: C41	Baker et al. (2005) and Ziegler et al. (2017)
	Fungia	N: C; CN: C, C1; C: C1, C1b; CS: C1, C1b, C41	Baker et al. (2005), Karako-Lampert et al. (2004), and Ziegler et al. (2017)
	Galaxea	CN: C, D; C: C1, C1b; CS: C1, C41	Baker et al. (2005) and Ziegler et al. (2017)
	Gardineroseris	CN: C, C39; C: C1, C39, D1, D1-4	Baker et al. (2005) and Ziegler et al. (2017)
	Goniastrea	CN: C1, C41, D1-4; C: C15, C41; CS: C15, D1, D1-4	Ziegler et al. (2017)
	Goniopora	N: C	Karako-Lampert et al. (2004)
	Hydnophora	CN: C	Baker et al. (2005)
	Leptoria	CN: C; C: D1	Baker et al. (2005), Baker et al. (2004), and Ziegler et al. (2017)
	Leptoseris	C: C1, C1mm, C15, C39, C63, D1-4	Ziegler et al. (2015a)
	Lobophyllia	CS: C1, C41	Ziegler et al. (2017)
	Montastrea	CN: C41	Ziegler et al. (2017)
	Montipora	N: C; CN: A, A1, C, C1b, C3, C3w, C38, D1-4; C: C3, C38; CS: A1, C3, C38, C41, D1, D1-4, D6	Baker et al. (2005), Baker et al. (2004), Karako-Lampert et al. (2004), and Ziegler et al. (2017)
	Mussa	CN: C	Baker et al. (2005)
	Mycedium	C: C1, C1b	Ziegler et al. (2017)
	Pachyseris	CN: A; C: C1, C1mm, C3, C39	Baker et al. (2005) and Ziegler et al. (2015a)
	Pavona	CN: C, C1, C15, C39, C41; C: C1, C39; CS: C1, C1b, C39, C83, C116, D1	Baker et al. (2005), Baker et al. (2004), and Ziegler et al. (2017)
	Plerogyra	CN: D	Baker et al. (2005)
	Plesiastrea	N: C41	Barneah et al. (2007)
	Pocillopora	N: A1, C, C1, C1^a, C1h, C1nn, C1oo; CN: A, A1, A1b, A1c, C, C3, C3w, C15, C19; C: A1, A1c, A21, B1, C#, C1#; C15, C98, C116, D1-4; CS: A1, A1c, C1, C1oo, C21, C41; S: A1, A21, C1^a, C19, D6, D17	Baker et al. (2005), Baker et al. (2004), Karako-Lampert et al. (2004), LaJeunesse et al. (2009), Santos and LaJeunesse (2006), Sawall et al. (2014), Ziegler et al. (2017), Ziegler et al. (2014b), and Ziegler et al. (2015b)
	Podabacia	CN: C; C: C1, C39	Baker et al. (2005) and Ziegler et al. (2015a)
	Porites	CN: A, C, C15; C: C15, C15n, C15o, C15p, C97, C99, C116, D1-4; CS: C22, D1, D1-4, D6	Baker et al. (2005), Baker et al. (2004), Ziegler et al. (2017), Ziegler et al. (2015a), and Ziegler et al. (2015b)
	Seriatopora	N: C, C3nt; CN: A, C, C163, C163a, C163b; C: A1, C163a; CS: A1; S: A1	Baker et al. (2005), Karako-Lampert et al. (2004), Nir et al. (2011), Santos and LaJeunesse (2006), and Ziegler et al. (2017)

(continued)

Table 5.2 (continued)

	Genus	Red Sea regions (underlined) and Symbiodiniaceae ITS2 types [a]	References
	Stephanocoenia	CN: C1	Ziegler et al. (2017)
	Stylophora	N: A, A1, C, C72; CN: A, A1, C, C21, C160, C161, C161a, C162a; C: A1, C1#, C116, Fr2-2; CS: A1, C19, C162, D1-4; S: C19	Baker et al. (2005), Baker et al. (2004), Barneah et al. (2007), Karako-Lampert et al. (2004), LaJeunesse et al. (2009), LaJeunesse (2001), Lampert-Karako et al. (2008); Santos and LaJeunesse (2006), and Ziegler et al. (2017)
	Symphyllia	CS: C41	Ziegler et al. (2017)
	Turbinaria	N: C, C1, C1n, C41; CN: C; C: C1; CS: C1, C1b, C41	Baker et al. (2005), Barneah et al. (2007), Karako-Lampert et al. (2004), and Ziegler et al. (2017)
Alcyonacea	*Anthelia*	N: C	Barneah et al. (2004)
	Cladiella	N: C	Barneah et al. (2004)
	Lithophyton	N: A, A10	Barneah et al. (2004) and LaJeunesse et al. (2009)
	Lobophytum	C: C65; CS: C65	Ziegler et al. (2017)
	Nephthea	N: A; C: A10	Barneah et al. (2004) and Ziegler et al. (2017)
	Paralemnalia	N: C	Barneah et al. (2004)
	Rhytisma	N: C	Barneah et al. (2004)
	Sarcophyton	N: C; CS: C65	Barneah et al. (2004) and Ziegler et al. (2017)
	Sinularia	N: C; C: C65; CS: C1, C1b, C65	Barneah et al. (2004) and Ziegler et al. (2017)
	Stereonephthya	N: A, A9	Barneah et al. (2007) and Barneah et al. (2004)
	Xenia	N: C; CN: C3; C: C3, C41, C115a, D1-4, D3, D5; CS: C3, C3.7, C3n, D3	Barneah et al. (2004) and Ziegler et al. (2017)
	Heteroxenia	N: C	Barneah et al. (2004) and Goulet et al. (2008b)
others	*Discosoma*	N: C1, D1-4	Kuguru et al. (2008)
	Rhodactis	N: C, C1, D, D1-4	Kuguru et al. (2008) and Kuguru et al. (2007)
	Tridacna	N: A, C	Richter et al. (2008)
	Millepora	N: A	Karako-Lampert et al. (2004) and Pochon et al. (2001)
	Amphisorus	N: C, Fr2, Fr5	Pawlowski et al. (2001) and Pochon et al. (2001)
	Marginopora	N: C	Pochon et al. (2001)
	Sorites	N: C, F2, Fr2, Fr4	Pawlowski et al. (2001), Pochon et al. (2006), and Pochon et al. (2001)
	Cassiopea	N: A1	LaJeunesse (2001)
	Waminoa	N: A11	Barneah et al. (2007)

Symbiodiniaceae clades correspond to the recently described genera: former clade A, *Symbiodinium*; former clade B, *Breviolum*; former clade C, *Cladocopium*; former clade D, *Durusdinium*; former clade F lineage Fr5, *Fugacium*; and representatives of clade F lineages Fr2 and Fr4 with yet undescribed genera

[a] Symbiodiniaceae detection methods used: DGGE (Barneah et al. 2007; Jessen et al. 2013; LaJeunesse et al. 2009; LaJeunesse 2001, 2005; Santos and LaJeunesse 2006; Sawall et al. 2014; Ziegler et al. 2014b; Ziegler et al. 2015a; Ziegler et al. 2015b), cloning & sequencing (Kuguru et al. 2008; Nir et al. 2011; Pawlowski et al. 2001; Pochon et al. 2006; Richter et al. 2008), RFLP (Baker et al. 2004; Barneah et al. 2004; Goulet et al. 2008b; Karako-Lampert et al. 2004; Kuguru et al. 2007; Lampert-Karako et al. 2008; Pochon et al. 2001), NGS (Ziegler et al. 2017)

host species than their IndoPacific counterparts (LaJeunesse et al. 2003). Data presented herein further points towards the Red Sea as a hot spot of Symbiodiniaceae diversity.

Cladocopium types C1 and C3 are believed to be at the basis of a series of regional adaptive radiation events in this genus in the miocene-pleistocene transition (LaJeunesse 2005; Thornhill et al. 2014). Repeated radiation led to high diversity within the genus *Cladocopium* (also reflected in its name) compared to the other Symbiodiniaceae genera and lineages (LaJeunesse et al. 2004b), and this pattern was also apparent in the Red Sea, with 69% of all types belonging to *Cladocopium*. The ancestral and globally occurring *Cladocopium* types C1 and C3 were also found in the Red Sea. While C1 represented the most widespread *Cladocopium* type in the Red Sea, *Cladocopium* C3 was rather uncommon, as opposed to other regions, where both types mostly occur in co-dominance (LaJeunesse et al. 2003). A different type, *Cladocopium* C41 so far only reported from Red Sea waters (LaJeunesse 2005; Pochon et al. 2001; Ziegler et al. 2017) was almost as ubiquitous as C1. Its sequence similarity with C1, from which it is separated by a single base pair difference in the ITS2 region, suggests a diversification event, specific to the Red Sea.

Some Symbiodiniaceae types are strongly associated with certain host taxa over large geographic ranges. For instance, the association of *Cladocopium* type C65 with Alcyoniidae extends beyond the Red Sea to other locations in the Western Indian Ocean (LaJeunesse et al. 2010) and along the GBR (Goulet et al. 2008a; LaJeunesse 2005; LaJeunesse et al. 2004b). Furthermore, *Seriatopora hystrix* associates with *Cladocopium* C3nt in both the Red Sea and the GBR. But while its association in the GBR is limited to symbionts from the genus *Cladocopium* (Bongaerts et al. 2010; LaJeunesse et al. 2003; Sampayo et al. 2007; Stat et al. 2008), it is additionally associated with symbionts from the genus *Symbiodinium* in the Red Sea. *Porites* in turn, though widely regarded a symbiont specialist coral for *Cladocopium* C3 in the Persian Gulf (Hume et al. 2013) and C15 in the IndoPacific (see Franklin et al. 2012), was found to be associated with a wide range of Symbiodiniaceae from the genera *Symbiodinium*, *Cladodopium*, and *Durusdinium* along the Red Sea coast. The diversity encountered in this genus in the Red Sea equals that found in Caribbean *Porites* (Finney et al. 2010; Green et al. 2010; LaJeunesse 2002, 2005), suggesting local, species-specific adaptive events driving host-symbiont specificity.

Patterns of variable host-symbiont association have previously been related to latitudinal gradients of temperature and inorganic nutrients (LaJeunesse 2002, 2005; LaJeunesse et al. 2004b; Loh et al. 2001; Macdonald et al. 2008). For instance, comparable to the reports of shifting Symbiodiniaceae communities to *Durusdinium* dominance for several host genera in warmer regions of the Red Sea (*Acropora*, *Astreopora*, *Diploastrea*, *Gardineroseris*, *Pavona*, *Pocillopora*, and *Porites*), *Acropora tenuis* in Australia associated with *Cladocopium* in the south (C3) and central region (C1, C3), i.e., the more temperate environments of the GBR, and with *Cladocopium* (C1) and *Durusdinium* (D1) in the northern warmer parts (LaJeunesse et al. 2004b; LaJeunesse et al. 2003). Latitudinal shifts in the association between types within a genus were observed in *P. verrucosa*, which associated with *Symbiodinium* A1 throughout its distribution range and with *Symbiodinium* A21 at the most southern location of the Red Sea (Sawall et al. 2014). These latitudinal shifts of Symbiodiniaceae assemblages in the Red Sea towards higher proportions of *Durusdinium* and *Symbiodinium* type A21 symbionts is also apparent along cross-shelf gradients, as evidenced by their presence in warmer, nutrient enriched and more turbid nearshore reefs, while being absent from colder offshore reefs in the central Red Sea (Ziegler et al. 2015b). Cross-shelf and habitat specific shifts between the genera *Cladocopium* and *Durusdinium* also occurred in coral communities in the GBR (Cooper et al. 2011a; Ulstrup and Van Oppen 2003), Palau (Fabricius et al. 2004), and Indonesia (Hennige et al. 2010). Moreover, corals harboring *Durusdinium* bleached less compared to those harboring other Symbiodiniaceaen lineages (Baker et al. 2004; Berkelmans and van Oppen 2006). Taken together, these observations suggest a competitive advantage for the respective coral host when associated with symbionts from the genus *Durusdinium* under warmer and nutrient enriched environmental settings (Berkelmans and van Oppen 2006; Stat and Gates 2011). However, not all host-symbiont combinations show this effect (Abrego et al. 2008), and the recently described 'heat-loving' *Cladocopium thermophilum* Hume, D'Angelo, Smith, Stevens, Burt & Wiedenmann, 2018 does not belong to the assumed heat-tolerant genus *Durusdinium* (Hume et al. 2015). This indicates that thermotolerance is not associated with a specific Symbiodiniaceaen lineage, but rather a type or species-specific trade that can be found in some members of all Symbiodiniaceaen lineages (Swain et al. 2017).

5.6 Coral Bleaching and Symbiosis Breakdown

Coral bleaching is the dissociation of the coral-Symbiodiniaceae symbiosis, during which the coral host loses large proportions of Symbiodiniaceae cells leading to the white, i.e., bleached appearance (Hoegh-Guldberg 1999). Global climate change induced sea surface warming and increased frequency and severity of temperature anomalies are the main causes for mass bleaching and global coral die-off events (Hoegh-Guldberg et al. 2007) that are becoming more frequent and devastating as evidenced by the third global coral bleaching event that affected coral reefs across the globe and devastated roughly one third (29%) of the coral reefs in the northern GBR (Hughes et al. 2018a; Hughes et al. 2018b). As most corals live very close to their upper thermal limit (Jokiel and Coles 1990), they are already susceptible to only small deviations from the long-term minima and maxima of temperature and other environmental factors (Kleypas et al. 1999). The effects of thermal stress can be aggravated when combined with eutrophication or imbalance of inorganic nutrients (Rädecker et al. 2015; Wiedenmann et al. 2012) and/or high solar irradiance (Fitt et al. 2001; Lesser 1996), which can also trigger bleaching on its own (Glynn 1993, 1996; Hoegh-Guldberg and Smith 1989; Krämer et al. 2013). Depending on the severity and duration of the stressor, corals can recover from bleaching events (e.g. Connell 1997). However, often coral bleaching leads to the death of the host, entailing mass mortalities and degradation of whole reefscapes (Hughes et al. 2018b; Sheppard 2003).

Several processes in the photosynthetic apparatus of Symbiodiniaceae are affected during coral bleaching. The breakdown of photosynthetic pathways and the continued absorption of light energy in photosystem II eventually exceed the capacity for non-photochemical quenching (Gorbunov et al. 2001; Wooldridge 2009) and ultimately lead to the production of reactive oxygen species (ROS) (Lesser 1996; Suggett et al. 2008; Tchernov et al. 2004; Warner et al. 1999). The different ROS impair and damage the structure and function of proteins, lipids, and DNA (Fey et al. 2005; Hideg et al. 1995; Martindale and Holbrook 2002; Smith et al. 2005). Consequently, ROS transgress to the coral host, causing further oxidative stress that is linked to the onset of coral bleaching (Lesser 1996; Smith et al. 2005) and initiation of apoptotic pathways in the host (Tchernov et al. 2011). Notably, recent studies suggest that other factors besides photodamage-induced ROS must be considered to explain observed bleaching phenomena (Tolleter et al. 2013; Diaz et al. 2016; Pogoreutz et al. 2017). As such, the elucidation of the cellular mechanisms underlying bleaching is an area of active investigation and critical to the design of meaningful interventions and mitigation strategies. Generally, coral species vary in their bleaching tolerance, with branching growth forms, as prevalent in e.g. Acroporids and Pocilloporids, displaying higher susceptibility than massive or encrusting species (Baird et al. 2009; Fitt et al. 2001; Loya et al. 2001; Stimson et al. 2002) and these trends are also apparent in bleaching events reported from the Red Sea (Table 5.3).

Similar to the flexible formation of host-symbiont relationships as a means to broaden the ecological niche, a resembling process has been formulated as a response to stress within individual colonies. The so-called 'adaptive bleaching hypothesis' was proposed as a mechanism through which the coral host can shift Symbiodiniaceae types to enhance its resilience to environmental changes (Buddemeier and Fautin 1993). This process is based on replacement of one Symbiodiniaceae type by another less abundant type ('shuffling') or by intake of exogenous Symbiodiniaceae from the environment ('switching') (Baker 2003). Background shuffling, i.e., changing proportions of Symbiodiniaceae types present in low abundances, may be a common phenomenon (McGinley et al. 2012) and the emergence of rare, less-abundant background Symbiodiniaceae can play a role during acute stress events (Boulotte et al. 2016; Lee et al. 2016), or as a source of adaptive potential over evolutionary time scales (Hume et al. 2016). But generally, many Symbiodiniaceae communities are stable over time (Thornhill et al. 2006a; Thornhill et al. 2006b), even during exposure to changing environmental conditions (Bongaerts et al. 2011), or when recovering from stress events (Goulet and Coffroth 2003; McGinley et al. 2012). Unfortunately, to date, there is a lack of information on the dynamics of the host-Symbiodiniaceae association during bleaching events in the Red Sea.

5.7 Coral Bleaching in the Red Sea

Coral reef ecosystems in the Red Sea thrive in warm seawater temperatures that exceed the tolerable limits of reef corals elsewhere (Kleypas et al. 1999). Caused by a selective bottleneck in the southern Red Sea possibly selecting for heat-resistant populations, the cooler northern part of the Red Sea is proposed to be a refuge for corals under global warming (Fine et al. 2013; Osman et al. 2018). In line with this, bleaching thresholds for corals in the Red Sea are higher than for most locations in the GBR, Indo-Pacific, and the Caribbean (Berkelmans 2002; Osman et al. 2018). In the last global report on the status of coral reefs in 2008, an estimated 82% of reefs in the Red Sea were classified at low risk (Wilkinson 2008). However, growth rates of *Diploastrea heliopora* have been declining since 1998 as a response to increased water temperatures, indicating that global warming also poses a major threat for Red Sea coral reefs (Cantin et al. 2010).

During the 1990s the Red Sea started to experience frequent SST anomalies and abrupt warming (Raitsos et al. 2011), and this period coincides with the earliest reports of coral bleaching in the Red Sea during the global coral bleaching event in 1998 (Table 5.3). Earlier *in situ* bleaching data from the region is wanting and large-scale surveys only started to take place under the umbrella of the Regional Organization for the Conservation of the Environment of the Red Sea and Gulf of Aden (PERSGA) after its foundation in 1995. However, using coral cores to estimate growth rates, a study by Cantin et al. (2010) suggests a possible thermal

Table 5.3 Record of bleaching events in the Red Sea with details on severity and affected coral taxa

Year	Red Sea region	Country	Location	Bleaching severity	Coral taxa affected and comments	References
1996/1997	south	Yemen	Al Khawkhah	High	Indirect observation of deceased colonies of *Goniastrea, Montipora, Porites* between survey years	Turak et al. (2007)
1998	central north, north	Saudi Arabia	Yanbu, Al-Wajh to Gulf of Aqaba	Low–medium	Low incidence, patchy bleaching, ~10%	DeVantier et al. (2005)
1998	central	Saudi Arabia	Rabigh to Yanbu	Medium–high	Severe bleaching on shallow reefs <6 m, up to 90% affected in Rabigh area, most affected, common taxa: *Acanthastrea*, *Acropora*, *Dipsastraea*, *Galaxea*, *Gardineroseris*, *Goniastrea*, *Leptastrea*, *Merulina*, *Millepora*, *Pocillopora*, *Porites, Stylophora, Tubastraea*	DeVantier et al. (2005)
1998	south	Eritrea	Massawa, Green Island	Medium–high	Water temperatures up to 40 °C, shallow and deep bleaching with subsequent mortality in shallow and recovery in deeper locations	ReefBase, NOAA, C. Wilkinson
1998?	south	Sudan	Dungonab Bay	–	Surveys in 2002 outside the bay found many dead colonies (*Galaxea* amongst others) and reefs in poor health state, possibly linked to previous bleaching	PERSGA (2003)
2002/2003	north	Israel	Gulf of Aqaba	–	sporadic bleaching of *Montipora*	Loya (2004)
2007	north / central north	Egypt, Jordan, Sudan	Fringing reefs	–	Low tides exposed reef flats with subsequent bleaching and mortality	Kotb et al. (2008)
2007	central north	Egypt	Rocky Island	–	Localized SST anomaly led to bleaching down to 20 m depth	Kotb et al. (2008)
2010	central	Saudi Arabia	Thuwal	Low–high	Cross-shelf gradient of bleaching with highest incidence nearshore of: Acroporidae, Agariciidae, Faviidae, Fungiidae, Merulinidae, Pectiniidae, Pocilloporidae, Poritidae, Siderastreidae, Oculinidae, Mussidae, Dendrophylliidae	Furby et al. (2013)
2010	central	Saudi Arabia	Thuwal	Variable	Spatial bleaching pattern of *Stylophora*; offshore reefs and nearshore protected areas unbleached	Piñeda et al. (2013)
2010	central	Saudi Arabia	Thuwal	High	Bleaching of all anemones in the area: *Heteractis, Entacmaea, Stichodactyla*	Hobbs et al. (2013)
2010/2011	north	Israel	Gulf of Aqaba	Medium	Mesophotic bleaching of *Stylophora* between 40 – 63 m, regular seasonal phenomenon?	Nir et al. (2014)
2010?	north	Egypt	Hurghada, Safaga, El Quesier	Low–medium	Based on the report, the year of bleaching is unclear. Medium bleaching: *Acropora*, *Montipora*, *Stylophora* Low bleaching: *Echinopora*, *Favia*, *Fungia*, *Galaxea*, *Pavona*, *Platygra*, *Pocillopora*	Ammar et al. (2012)
2015	central	Saudi Arabia	Thuwal	Low–high	Low bleaching at offshore and midshore locations, high bleaching nearshore	Monroe et al. (2018); Roik et al. (2015)
2015	central south	Saudi Arabia	Al Lith	High	All shallow corals affected nearshore to offshore, partial bleaching down to 20 – 30 m	Osman et al. (2018)

anomaly in the central Red Sea as early as 1941/1942, when growth rates intermittently decreased by 44%.

The first recorded coral mortality in the Red Sea, which was later attributed to a bleaching event, dates back to Khawkhah (Yemen) where areas of large *Goniastrea retiformis*, *Montipora* spp., and *Porites* spp. succumbed to bleaching between 1996 and 1997 (Turak et al. 2007). While this seemed to be a local event, the first large-scale coral bleaching in the Red Sea was reported 1 year later during the 1998 global coral bleaching. A census of the central to northern Saudi Arabian Red Sea coast during summer and fall of 1998 found 10% of surveyed reefs to be affected by bleaching (DeVantier et al. 2005). The highest incidence occurred on shallow reefs (<6 m) between Rabigh and Yanbu, at water temperatures above 31 °C, which is 2 °C above the mean monthly average. In the area around Rabigh bleaching affected hard, soft, and fire corals with recently dead and bleached colonies accounting for up to 90% of the total coral cover (DeVantier et al. 2005). The most affected genera included *Acropora*, *Dipsastraea*, *Galaxea*, *Goniastrea*, *Millepora*, *Pocillopora*, and *Porites* (DeVantier et al. 2005). The reefs outside Dungonab Bay on the western shore of the Red Sea (Sudan) at roughly the same latitude were possibly affected by this event too, as was suggested from their poor health state during surveys in 2002 (PERSGA 2003). At the same time, the northern Red Sea (i.e., coral reefs in Egypt) (Kotb et al. 2004), the areas to the north of Yanbu, and areas with coastal upwelling (DeVantier et al. 2005) were largely unaffected.

Although reefs in the northern Red Sea largely escaped the 1998 bleaching event, coral cover was still declining in some regions between 1998 and 2004 (Kotb et al. 2004). These changes were attributed to local anthropogenic stressors, such as coastal development, pollution, and tourism related activities (Kotb et al. 2004), as well as sporadic coral bleaching of *Montipora* spp. in the Gulf of Aqaba in the summers of 2002 and 2003 (Loya 2004). After 1998, coral recovery along the Sudanese and Yemeni coastlines varied from almost no recovery to areas with high levels of recruitment and regrowth until 2007 (Klaus et al. 2008; Kotb et al. 2004). In March 2007 extremely low tides exposed reef flats along large stretches of coast in Egypt, Jordan, and Sudan leading to extensive coral bleaching and mortality (Kotb et al. 2008). In October of the same year a localized warm water event caused further coral bleaching down to 20 m depth on the offshore archipelago of 'Rocky Island' in south Egypt (Kotb et al. 2008).

The next record of coral bleaching dates back to 2010, where coral reefs in the central Saudi Arabian Red Sea near Thuwal were exposed to up to 11 degree heating weeks (Furby et al. 2013). Bleaching increased with proximity to shore and in shallow areas, where the majority of corals was affected; Oculinidae and Agaricidae being the worst impacted with up to 80 – 100% bleaching (Furby et al. 2013). Moreover, all anemone species bleached during the bleaching event, incl. *Heteractis magnifica*, *Entacmaea quadricolor*, *Stichodactyla haddoni* (Hobbs et al. 2013). Nearshore reefs experienced subsequent mortality of many taxa, while midshore and offshore reefs recovered to levels close to before the bleaching (Furby et al. 2013). A study investigating spatial patterns of bleaching in *Stylophora pistillata* largely supported the observations by Furby et al. (2013) and highlighted fine scale bleaching patterns with nearshore protected corals being less affected than those from the exposed side of the same reef, stating that: "Corals from the mildest and the most extreme thermal environments escape mortality" (Piñeda et al. 2013). At the same time *S. pistillata* at mesophotic depth (40 - 63 m) in the Gulf of Aqaba underwent repeated seasonal coral bleaching and recovery during the summers of 2010 and 2011 (Nir et al. 2014), questioning the role of deep reefs as coral refuges at least in this location (Fine et al. 2013; Glynn 1996). One more study published in 2012 reports on coral bleaching along the central Egyptian coast from northern Hurghada to El Quseer mostly affecting corals from the genera *Stylophora*, *Galaxea*, *Acropora*, and *Montipora*, but it is unclear when this bleaching was observed (Ammar et al. 2012).

The following El Niño-Southern Oscillation (ENSO) event during 2015 again hit coral reefs in the central and southern Red Sea (Monroe et al. 2018; Osman et al. 2018; Roik et al. 2015). Preliminary surveys along the Saudi Arabian coast showed coral bleaching in the central south around 20°N, with reefs up to 60 km offshore and down to >20 m being severely affected (Osman et al. 2018). The reefs around Thuwal (22°N) followed cross-shelf bleaching patterns comparable to the reports from 2010 (Furby et al. 2013; Monroe et al. 2018), while reefs in the Yanbu area (24°N) and those north of Yanbu seemed largely unaffected (Osman et al. 2018). Overall, bleaching susceptibility of coral genera throughout the Red Sea was comparable to other geographic provinces, with fast-growing branching Acroporids and Pocilloporids being affected fastest and least likely to recover. However, at the most impacted locations bleaching was a mass phenomenon that affected all coral species.

As highlighted by the increasing numbers of bleaching reports, coral reefs in the Red Sea are impacted by global climate change. Although phase shifts from coral-dominated to algal-dominated habitats have not been reported from the Red Sea yet, comparative surveys spanning the entire Red Sea coast over 2 decades indicate increasing coral community homogenization, loss of rare coral species, and a general decline in coral colony sizes (Riegl et al. 2012). Further, the 2010 bleaching event resulted in almost complete local extinction of certain taxa in some reefs and declines in diversity and coral cover in many reefs (Furby et al. 2013). Of note, bleaching is not the only cause of coral decline in the Red Sea. Heavy construction activities around urban areas along the coast, oil spills, landfilling, pollutant discharge, and effluents from desalination centers continue to threaten coastal ecosystems in the Red Sea, but observations that assess the effect of these stressors are rare (Ziegler et al. 2016) and largely anecdotal.

5.8 Outlook: What Can We Learn from Red Sea Algal Symbionts in Regard to 'Future Oceans'?

Coral host-Symbiodiniaceae associations provide the foundation of reef ecosystems and studying their relationships is the key to understanding the implications of changing environmental conditions on coral reef functioning. One of the main challenges in Symbiodiniaceae research to date is the scarcity of properly described Symbiodiniaceae species and the difficulties in assigning evolutionarily and ecologically distinct lineages as species. Although the ITS2 marker has long been used for this purpose and reasonable validity is attested to the resolution of Symbiodiniaceae ITS2 types as species (Sampayo et al. 2009; Thornhill et al. 2007), a multi-copy genetic marker such as ITS2 poses various challenges for diversity analyses (Arif et al. 2014; LaJeunesse and Thornhill 2011). At the same time, and in combination with high throughput next-generation sequencing approaches, such intragenomic diversity may be used to resolve between symbiont taxa at a level far surpassing previous approaches (Hume et al. 2019). In addition, efforts in developing alternative molecular markers will benefit from Symbiodiniaceae genomes as an available resource (Aranda et al. 2016; Lin et al. 2015; Shoguchi et al. 2013). Another line of research to overcome these challenges is the establishment of cultured isolates of Symbiodiniaceae from the Red Sea to further address Symbiodiniaceae species' physiological and biochemical properties.

Despite the long research tradition in the northern Red Sea, specifically in the Gulf of Aqaba, large parts of the Red Sea remain difficult to study due to limited access. This is highlighted by the limited number of studies on Symbiodiniaceae diversity, their distribution and sampling periods, but also the general lack of ecological data, such as bleaching observations from the Red Sea. Thus, we advocate extended sampling efforts on both coasts along the entire Red Sea coast to enhance the understanding of Symbiodiniaceae assemblage patterns in this understudied, but globally important region. The large diversity of Symbiodiniaceae communities in the Red Sea offers a unique opportunity to study the ecological performance of distinct host-symbiont combinations and shuffling/switching events in relation to changing environmental conditions, but only few studies have begun to do so (Sawall et al. 2014; Ziegler et al. 2015b, 2018). Furthermore, the presence of an apparently endemic, but regionally common type such as *Cladocopium* C41 suggests regional adaptation and speciation processes (Ziegler et al. 2017). This offers the opportunity to investigate the origin of symbionts and adaptation to local conditions (but see Hume et al. 2016).

Distribution patterns of Symbiodiniaceae in the Red Sea support the putative role of members of the genus *Durusdinium* in thermally challenged environments that were previously observed elsewhere (Fabricius et al. 2004; Hennige et al. 2010). First, *Durusdinium* occurs in warm nearshore locations in the Red Sea, and second, it becomes more ubiquitous among host species in the warmer southern Red Sea. Beyond validating and extending the thermal tolerance of *Durusdinium* geographically, the Red Sea provides a good place to identify other heat resistant symbiont types. One of these may be found in *Symbiodinium* A21, which followed a similar pattern of occurrence to that of *Durusdinium*. These observations further warrant comparative investigations into the molecular, biochemical, and physiological basis underlying thermotolerance of Symbiodiniaceae. The application of functional genomic tools will aid in elucidating the molecular underpinnings of resilience to the extreme environmental conditions in the Red Sea and thus contribute to a broader understanding of the impacts of climate change on coral reef ecosystems on a global scale.

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