Symbiodiniaceae Genetic Diversity and Symbioses with Hosts from Shallow to Mesophotic Coral Ecosystems

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Abstract

Multiple members of the phylum Cnidaria (e.g., corals, octocorals, and sea anemones) and other organisms such as mollusks, foraminiferans, and sponges associate with unicellular dinoflagellates belonging to the family Symbiodiniaceae. These symbioses are often obligatory, and for shallow coral reefs, form the foundation of the ecosystem. This chapter presents the current knowledge of Symbiodiniaceae genetic distinction and the ramifications of different Symbiodiniaceae genotypes on the host-Symbiodiniaceae entity, the holobiont. Since the early 1990s when molecular techniques using polymerase chain reaction (PCR) enabled rapid resolution of Symbiodiniaceae, both within and between host species, knowledge on Symbiodiniaceae diversity has grown exponentially. Subsequently, application of multiple molecular techniques and genetic markers enabled the analysis of Symbiodiniaceae diversity from broad genera (formerly cladal) groupings to the individual genotype. Previous lack of a standard Symbiodiniaceae nomenclature, however, led to naming redundancies and utilization of the same terminology to discuss different levels of taxonomic resolution. This ambiguity has now been addressed. Knowledge of Symbiodiniaceae genetic diversity enables understanding and puts in context the host-Symbiodiniaceae genotypic combination. Deciphering the holobiont's ecology, including the holobiont's responses to environmental conditions brought about by global climate change, requires knowledge of Symbiodiniaceae identity, as does contemplating the applicability of the deep reef refugia hypothesis. This review accentuates the current meager knowledge of Symbiodiniaceae genetic diversity in mesophotic coral ecosystems in general, which is confined to scleractinian and antipatharian coral hosts, and the lack of data on Symbiodiniaceae genotypes in other symbioses.

Keywords

Mesophotic coral ecosystems · Zooxanthellae · Octocoral · Sea anemone · Sponges · *Symbiodinium*

30.1 Introduction

The mesophotic zone is arbitrarily defined as occurring between 30 m to a depth in which light in the water column is too low to sustain photosynthesis (Hinderstein et al. 2010), either in macroalgae or hosts that rely on unicellular dinoflagellate photosymbionts, formerly attributed to the genus *Symbiodinium* and now included in the family Symbiodiniaceae (LaJeunesse et al. 2018). From the definition, two points emerge. First, although we ascribe depth ranges to mesophotic coral ecosystems (MCEs), the depth limits of MCEs rely more on light quality (light spectra) and quantity (irradiance levels), which vary at geographic (e.g., Caribbean vs. Red Sea) and local (e.g., a region with low vs. high eutrophication) scales. Second, even though Symbiodiniaceae containing hosts constitute an important aspect of MCEs, knowledge about Symbiodiniaceae genotypes on MCEs is sparse. If we are to understand the ecology of MCEs, we need to learn more about the relationships between Symbiodiniaceae and their host taxa, with whom Symbiodiniaceae collectively form entities, referred to as holobionts (Rohwer et al. 2002). A key to this understanding is knowing the genotypes involved in the symbioses.

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Symbiodiniaceae engage in symbioses with multiple members of the phylum Cnidaria such as scleractinian corals, octocorals, and sea anemones. In addition, Symbiodiniaceae associate with mollusks such as giant clams, *Tridacna* (Trench et al. 1981) and queen conch, *Lobatus* (previously *Strombus*) *gigas* (Banaszak et al. 2013), sponges belonging to the family Clionaidae (Hill et al. 2011), and foraminiferans (Lee et al. 1995). The host-Symbiodiniaceae entity can also include a consortium of other symbioses, both ecto- and endosymbionts, such as fishes (Liberman et al. 1995), crabs and shrimp (Glynn 1980), bivalves (Mokady et al. 1998), fungi (Bentis et al. 2000), endolithic algae (Odum and Odum 1955; Shashar et al. 1997), and bacteria (Rohwer et al. 2002; Shirur et al. 2016). Of the various symbionts, the dinoflagellate Symbiodiniaceae are key, forming obligatory symbioses with many of their hosts. Therefore, Symbiodiniaceae play a pivotal role in the holobiont entity, and, in the case of coral reefs, the existence of an entire ecosystem.

In the spectrum of benefits gained from mutualism (Douglas 2010), Symbiodiniaceae, through inorganic carbon fixation, provide their hosts with access to photosynthetic products (Muscatine and Porter 1977) and, in the case of calcifying hosts, affect their calcification (Goreau and Goreau 1959; Pearse and Muscatine 1971). The host provides its metabolic wastes (Muscatine and D'Elia 1978), an asset in oligotrophic seas, and may also protect its endosymbiotic Symbiodiniaceae from antagonists (Douglas 2010). Because Symbiodiniaceae translocate photosynthetic products, different Symbiodiniaceae may vary in their photosynthetic output, response to environmental conditions, and a multitude of other aspects influenced by their genetic makeup. Hence, to understand the ecology and physiology of host-Symbiodiniaceae symbioses found in MCEs, it is imperative to incorporate genetic knowledge about Symbiodiniaceae.

30.2 Symbiodiniaceae Genotypic Identity Affects Understanding MCEs

For organisms that host Symbiodiniaceae at any depth, including MCEs, determining and including Symbiodiniaceae genetic information are critical for data interpretation. The scleractinian corals *Seriatopora hystrix* and *Stylophora pistillata*, and studies conducted in the Gulf of Eilat/Aqaba (GOE/A) in the Red Sea, illustrate this point. In the northern tip of the GOE/A, *S. hystrix* occurs from 0 to 65 m depths (Nir et al. 2011). Within this depth range, *S. hystrix* hosts Symbiodiniaceae within the genus *Cladocopium* (formerly Clade C, LaJeunesse et al. 2018) that most closely resemble the former type C3nt, now referred to as *Cladocopium* C3nt (Nir et al. 2011). Despite a tenfold decrease in light intensity between 20 and 50 m, chlorophyll *a* and *c* content per *Cladocopium* cell and photochemical efficiency did not vary with depth (Nir et al. 2011). Conversely, host morphological characteristics of branch diameter and corallite structure and spacing did vary (Nir et al. 2011). Consequently, the host modifications led to changes in the holobiont, which potentially negated the need for *Cladocopium* to change parameters associated with their photosynthetic machinery.

In *S. pistillata,* which occurs down to depths of 70 m in GOE/A (Mass et al. 2007), a different story emerged. Winters et al. (2009) evaluated *S. pistillata* from 2 to 30 m and found that the Symbiodiniaceae in *S. pistillata* in shallow water (2 m) differed in multiple ways from the Symbiodiniaceae in colonies from deeper habitats (30 m). Symbiodiniaceae cells in shallow-water colonies were smaller in diameter and deeper inside the host tissue compared to those in the colonies at 30 m (Winters et al. 2009). Symbiodiniaceae in the colonies found at 30 m had more chlorophyll per algal cell compared to the Symbiodiniaceae in colonies at 2 m (Winters et al. 2009). Juxtaposed on the parameter differences is the fact that the Symbiodiniaceae in the *S. pistillata* colonies at 2 m belonged to the genus *Symbiodinium sensu stricto* (formerly clade A, LaJeunesse et al. 2018) compared to *Cladocopium* found in colonies at 30 m (Winters et al. 2009). Hence, in *S. pistillata* over depth, the host-symbiont genotypic combination changes, with the different Symbiodiniaceae genotypes possessing different characteristics. Therefore, in the same geographic area, two coral hosts exhibited holobiont variation from shallow to mesophotic reefs, although the mechanisms for the holobiont modifications differed.

Identifying Symbiodiniaceae is particularly important when Symbiodiniaceae attributes are measured. For example, in a study on *S. pistillata* colonies at 3 versus 30 m, the shallow water colonies had lower Symbiodiniaceae density and chlorophyll *a* concentrations per algal cell compared to the deep colonies (Cohen and Dubinsky 2015). Reciprocally transplanting *S. pistillata* between 3 and 30 m led to changes in Symbiodiniaceae density and chlorophyll levels. Without identifying the Symbiodiniaceae, however, one does not know whether the same Symbiodiniaceae acclimated to new environmental conditions. Alternatively, Symbiodiniaceae shuffling (Baker 2003) may have occurred, with the transplanted *S. pistillata* now predominantly hosting Symbiodiniaceae dominating that depth. Likewise, in a study on *Euphyllia paradivisa* from a MCE in the GOE/A, Symbiodiniaceae photosynthetic efficiency was measured at both natal depths and transplanted shallow-water locations (Eyal et al. 2016). Eyal et al. (2016) concluded that the Symbiodiniaceae displayed "a high photosynthetic plasticity." Unfortunately, the Symbiodiniaceae genetic identity was not determined, thus leaving a knowledge gap in understanding and interpreting the results.

30.3 Current Knowledge of Symbiodiniaceae Genetic Diversity

The identity of Symbiodiniaceae has stumped researchers since 1881 when Brandy proposed the term zooxanthellae to describe the yellowish/brown balls (Fig. 30.1) found in animals and yet distinct from the animals (cited in Blank and Trench 1986). Other researchers also referred to symbiotic diatoms by the same name, leading to confusion in the literature about terminology related to symbiotic algae (reviewed in Trench and Blank 1987). To this day, the colloquial term zooxanthellae (singular: zooxanthella, e.g., zooxanthella density) appears frequently in the literature in reference to any brown microalga that lives in symbiosis with corals, clams, mollusks, flatworms, jellyfish, sponges, etc. Since this common term is not based on any distinct morphological or genetic characteristics, Blank and Trench (1985) suggested that it should be phased out in favor of referring to a *Symbiodinium* genus.The genus *Symbiodinium*, however, has also been problematic. Freudenthal (1962) named the dinoflagellate algae from the upside down jellyfish, *Cassiopeia* sp. as *Symbiodinium microadriaticum*. Yet, without a species holotype specimen, the species and the genus were invalid. The recent work of LaJeunesse et al. (2018) has established the family Symbiodiniaceae which currently includes seven genera. Although several Symbiodiniaceae species are now officially named (LaJeunesse 2017, and references within; LaJeunesse et al. 2018), Symbiodiniaceae sequence comparisons, whether directly with sequence alignment or indirectly by visualizing DNA fragments via techniques such as restriction fragment length polymorphism (RFLP; Rowan and Powers 1991a, b, 1992), denaturing gradient gel electrophoresis (DGGE; LaJeunesse 2001), or single- strand conformational polymorphisms (SSCP; Fabricius et al. 2004), have enabled researchers to distinguish between Symbiodiniaceae (Table 30.1). Initially, Rowan and Powers (1991a, 1992) placed Symbiodiniaceae into what they termed as “groups,” assigning alphabetical letters (A, B, C) to distinguish between the groups. Rowan (1991) also referred to these groups as “strains” and “RFLP genotypes.” Calling these groups “clades” appeared in publications from the Eighth International Coral Reef Symposium held in 1996 (Baker and Rowan 1997; Baker et al. 1997; Goulet and Coffroth 1997) and thereafter (e.g., Bythell et al. 1997).

Once *Symbiodinium* clades became a common delineation method, and as molecular techniques matured and became financially accessible, researchers utilized different DNA regions to distinguish within a clade (Table 30.1). Unlike with RFLP of nuclear genes that encode small ribosomal subunit RNA (ssRNA), even when using the same DNA region, different techniques and/or machines precluded visual comparison of banding patterns. For example, the polymerase chain reaction (PCR) products of the nuclear ribosomal DNA internal transcribed spacer regions 1 and 2

Fig. 30.1 An *Agaricia lamarcki* Milne Edwards & Haime, 1851 coral colony (**a**). This scleractinian coral species has a wide bathymetric distribution on Caribbean reefs and is one of the most representative species of the MCEs in Puerto Rico. Close-up photos of individual polyps of the *A. lamarcki* colony in which Symbiodiniaceae cells appear as olive (**b**) and brown (**c**) dots. Isolated Symbiodiniaceae cells from the *A. lamarcki* colony with phase-contrast microscopy (**d**). The *A. lamarcki* colony was collected by A. Veglia and J. Garcia-Hernandez from Turrumote Reef, La Parguera, Puerto Rico from 17 m depth. (Photo credits for all panels: J. Garcia-Hernandez and N. V. Schizas)

Table 30.1 Symbiodiniaceae genetic differentiation. Symbiodiniaceae genotypic levels of resolution, from broad to specific, utilizing specific DNA regions and techniques

	Broad	→		Specific
Resolution level	Genus	Lineage (species, type)	Population	Individual
DNA region used	ssRNA[1]	ITS1& ITS2[4]	*psb*Ancr [7]	Whole genome[9]
	lsRNA[2]	cp23S-rDNA[5]	Microsatellites[8]	Microsatellites[8]
	Mt*cox*1[3]	Microsatellite flanker regions[6]		
Molecular technique	PCR	PCR, DGGE, and sequencing[4]	PCR	DNA fingerprinting[9]
	RFLP[1]	PCR, SSCP, and sequencing[11]	Sequencing	PCR and/or sequencing
	Sequencing[1]	PCR, cloning, and direct sequencing[12]	RAPD[14]	RAPD[13]
	rtPCR[10]	Pyrosequencing[13]		Clonal cultures and allozymes[15]

Acronyms from left to right include: DNA encoding for small (ssRNA) or large (lsRNA) subunit ribosomal RNA, mitochondrial protein-coding gene (cytochrome oxidase subunit I [*cox* 1], Mt*cox*1), nuclear ribosomal DNA internal transcribed spacer region 1 (ITS1) and 2 (ITS2), chloroplast large subunit (23S)-rDNA (cp23S-rDNA), non-coding region of the plastid *psb*A minicircle (*psb*Ancr) DNA, *PCR* polymerase chain reaction, *RFLP* restriction fragment length polymorphism, *DGGE* denaturing gradient gel electrophoresis, *SSCP* single-strand conformational polymorphisms, *rtPCR* real- time PCR, *RAPD* random amplified polymorphic DNA

Representative papers: [1]Rowan and Powers (1991a), [2]Baker and Rowan (1997), [3]Takabayashi et al. (2004), [4]Hunter et al. (1997) and LaJeunesse (2001), [5]Santos et al. (2002), [6]Finney et al. (2010), [7]LaJeunesse and Thornhill (2011), [8]Santos et al. (2003), [9]Goulet and Coffroth (2003b), [10]Yamashita et al. (2011), [11]Fabricius et al. (2004), [12]Apprill and Gates (2007), [13]Arif et al. (2014), [14]Belda-Baillie et al. (1999), [15]Baillie et al. (1998)

(ITS1, ITS2) have been separated using DGGE (LaJeunesse 2001) or SSCP (Fabricius et al. 2004). In addition, even with the same technique, such as DGGE, DNA fragment migration patterns may differ between electrophoresis systems (Thornhill et al. 2010). Therefore, the techniques utilized for within Symbiodiniaceae genera resolution limit comparisons of banding patterns between studies and require DNA sequence comparisons, assuming that the segments of the chosen DNA regions overlap between studies.

Furthermore, without the recent cohesive framework or guidelines, the different DNA regions and/or names utilized by multiple investigators resulted in an inconsistent and often redundant nomenclature. For example, type C1 in LaJeunesse et al. (2003) is the same as subclade C1 (van Oppen et al. 2001), while C3i (LaJeunesse et al. 2003) was called subclade C2 by van Oppen et al. (2001), and the subclade *Symbiodinium* C15, based on ITS1, is the same as Clsu10 which was identified using large subunit rDNA (Stat et al. 2009). Some papers pointed out the equivalency nomenclature for their studied symbioses (e.g., LaJeunesse et al. 2003; Stat et al. 2015), but others did not, leaving the reader on their own to decipher Symbiodiniaceae genetic differences and similarities. Other papers presented operational taxonomic units (OTUs) with notations specific to that data (Arif et al. 2014; Gonzalez-Zapata et al. 2018) or did not name Symbiodiniaceae and resorted to listing sequence identification numbers given by Genbank (Diekmann et al. 2002).

While the cladal naming was in use, at the forefront of the subcladal distinction were '*Symbiodinium* types' (LaJeunesse 2001), based primarily on ITS1 and ITS2, and named by combining the clade nomenclature with numbers and letters, e.g., C1:3a (Goulet et al. 2008). Nevertheless, beyond the cladal level distinction, the same term was sometimes used to refer to different hierarchical levels. For instance, in a recent publication on *Symbiodinium* in the scleractinian coral *Agaricia undata* on Caribbean MCEs, the term "*Symbiodinium* clade" was used to refer to "*Symbiodinium* type" C3 (Gonzalez-Zapata et al. 2018). In addition, the term "phylotype" was often used when referring to *Symbiodinium* types (Brading et al. 2011). Using the same terms for different levels of resolution can lead to confusion in the research community. With the new family Symbiodiniaceae and the comprehensive delineation of genera and resolution within them (LaJeunesse et al. 2018), it would behoove the research community to utilize this nomenclature and to relate prior Symbiodiniaceae identification to this nomenclature.

Over the years, several review articles summarized Symbiodiniaceae genetic distinction, from the previously used broad cladal level to the individual genotype (e.g., Baker 2003; Coffroth and Santos 2005; Pochon and Gates 2010; Thornhill et al. 2017). Regardless, information on Symbiodiniaceae diversity in hosts inhabiting MCEs is sparse, particularly at the population or finer resolution scales. For example, the vast majority of Symbiodiniaceae population studies to date, summarized in Table 1 of Thornhill et al. (2017), investigated Symbiodiniaceae from hosts located in shallow water (< 15 m) or did not reveal the sampling depths. In addition, studies that utilized total genomic DNA fingerprinting to differentiate between individual Symbiodiniaceae genotypes in the octocoral *Plexaura kuna* collected samples up to the lower end of its depth distribution, 17 m (Goulet and Coffroth 2003a) and from *P. kuna* fragments transplanted to >20 m (Goulet and Coffroth 2003b). With growing interest and access to MCEs, Symbiodiniaceae identification in hosts from MCEs, from the genus level to finer levels of identification, is gaining momentum, although current Symbiodiniaceae genetic identification is confined to scleractinian and black coral (antipatharian) symbioses (Table 30.2).

Table 30.2 Symbiodiniaceae in hosts for which data are available from MCEs. Since the studies were performed prior to the systematic revision of Symbiodiniaceae, the clades and types appearing in those studies are presented. For a given host species, Symbiodiniaceae genotypes are also listed for shallow (0–10 m), mid (10–20 m), and deep (20–30 m) depths, where available, with types that occur both in mesophotic and shallower reefs accentuated in bold

Family	Coral species	Location	Depth (m)					Reference
			Shallow (0–10)	Mid (10–20)	Deep (20–30)	Upper mesophotic (30–60)	Lower mesophotic (60–200)	
Scleractinian corals								
Acroporidae	*Acropora elegans*	GBR	A, C1, **C3**, C3h, C3i, C3k, C21, D, D1	C1, **C3**, C3k, D1		**C3**		1
	Montipora spp.	GBR	**C3**, C15, **C17**, C21, C26, C26a, C31, C73	C26a, C61		**C3**, **C17**	**C3**	1
Agariciidae	*Agaricia agaricites*	Curaçao	C3, **C3*N2*, C3*N3***	C3, **C3*N2*, C3*N3***		**C3*N2*, C3*N3***		2
	A. grahamae	Curaçao				C11, C11*N4*	C11, C11*N4*	2
	A. lamarcki	Curaçao		C3, C3d, C3*N*6, C3*N*7, **C11, C11*N4***	C3, C3d, C3*N*6, C3*N*7, **C11, C11*N4***	**C11, C11*N4***		2
		Mona Isl., PR			C3, C3d, C11*N4*, C11*N*10 , D1a*N14*	C11, C11*N4*	C11, C11*N4*	3
		Parguera, PR			C3, C3d, C11*N4*, D1a*N*14 *	C11, C11*N4*	C11, C11*N4*	3
		St. Croix, USVI			C3, C11*N4*, D1a*N*14 *	C11, C11*N4*	C11, C11*N4*	3
		St. Thomas, USVI			C3, C3d, D1a*N14*			3
	Helioseris cucullata	Curaçao				C11*N*4		2, 4, 5
	Leptoseris amitoriensis	Central Red Sea				C1		6
	L. explanata	Central Red Sea	D1a		D1a	C15, C39, C63		6
	L. foliosa	Central Red Sea				C1		6
	L. hawaiiensis	Central Red Sea				C1mm		6
		GBR	C1	C3h, C21			C3i (C1/C3)	2
		Hawaii					C1, C1v1e, C1v6, C1v18	7
	L. papyracea	Hawaii					C1, C1v1b, C1v1c, C1v3, C1v8	7
	L. scabra	Hawaii					C1, C1c/C45, C1v1d	7
	L. tubulifera	Hawaii					C1, C1c/C45, C1v1e	7
	Leptoseris spp.	Hawaii				C1, C1b, C1c, C27		8
	Leptoseris sp. 1	Hawaii					C1, C1v1b, C1v1c, C1v8	7

(continued)

Table 30.2 (continued)

Family	Coral species	Location	Depth (m)					Reference
			Shallow (0–10)	Mid (10–20)	Deep (20–30)	Upper mesophotic (30–60)	Lower mesophotic (60–200)	
	Pachyseris speciosa	GBR	C3h	C3h, C21		C3k		1
		Central Red Sea		**C3**, **C39**	**C3**, **C39**	**C3**, **C39**, C1mm		6
	Pavona spp.	GBR	C1, C1b, C3h, C27	C3h, C21		C3, C3k		1
Astrocoeniidae	*Madracis carmabi*	Curaçao			B7			5, 9
	M. decactis	Curaçao	B7	B7	B7			5, 9
	M. formosa	Curaçao	**B7**	**B7**	**B7**	**B7**, B15	B15	5, 9
	M. mirabilis	Curaçao	B7, B13	B7, B13	B7, B13			5, 9
	M. pharensis	Curaçao	B7	B7	B7	B15	B15	5, 9
	M. senaria	Curaçao	**B7**	**B7**	**B7**	**B7**		5, 9
Fungiidae	*Fungia* cf. *danai*	GBR	C1, C21, C3h	C1, C3h		C3i (C1/C3), C3k		1
	Podobacia sp.	Central Red Sea	C1	C1	C1, C39			6
Lobophylliidae	*Echinophyllia aspera*	GBR	C3, C3h, C3ha, C21	C1, C3h		C3k		1
Montastraeidae	*Montastraea cavernosa*	Bahamas	**C3**, **C3b**, Mcav1, 7, 9	**C3**, **C3b**, C3e, C21.**C3 d**, C1, Mc`av1, 2, 10, 11	**C3**, **C3b**, C3e, C21. C3 d, C1, Mcav1, 2, 3, 7, 9	**C3**, **C3b**, **C3d**, C21. C3d, Mcav3	**C3**, **C3b**, C21.**C3d**, Mcav4, 5, 6, 8, 9	10
		Curaçao	**C3**, **C3U1**	**C3**, **C3U1**		**C3**, C3*N25,* **C3U1**, C3U1, C3U2,	**C3**, C3*N*25, **C3U1**	5
		Florida Keys	B1, **C3**, D1a	**C3**		**C3**		11
		Bermuda	**C3**	**C3**		**C3**		11
		St. Thomas, USVI	**C3**	**C3**		**C3**		11
		FGB, GOM		**A13, C1.168, Cn.1, Cn.2, Cn.3**, Cn.4		**A13, C1.168, Cn.1, Cn.2, Cn.3**		12
Oculinidae	*Galaxea astreata*	GBR	C1, C21, D1a	C1, D1a		C3		1

(continued)

Table 30.2 (continued)

Family	Coral species	Location	Depth (m)					Reference
			Shallow (0–10)	Mid (10–20)	Deep (20–30)	Upper mesophotic (30–60)	Lower mesophotic (60–200)	
Pocilloporidae	*Seriatopora hystrix*	GBR	C3n-t, C120, C120a, C1m-aa	**C3**, C3n-t	C120, C3n-t, C3-ff	**C3n**, C3n-hh		1
		NE Australia	D1a		C1, C1/C1#			13
		NW Australia (Indian Ocean)	D1a	D1a	D1a	C1, C1-like		13, 14
		Ryukyu Islands, Japan	**C1-like, C59, C78a-like**	**C1-like, C59, C78a-like**	**C1-like, C59, C78a-like**	**C1-like,** C3, **C59, C78a-like**		15
		GOE/A, Red Sea	**C3nt- like**	**C3nt- like**	**C3nt- like**	**C3nt-like**		16, 17
	Stylophora pistillata	GOE/A, Red Sea	A1, A4	A1	A1, C72	C1, C1s, C21s, C21t	C21t, C72s	18, 19, 20, 21
Poritidae	*Porites astreoides*	Bermuda	**A4**, B1	**A4, A4a**		**A4, A4a**		22
		Curaçao	**A4, A4a, B1, C80, C80*N41*, C80U11**			**A4, A4a, B1, C80, C80*N41*, C80U11**		5
		Florida Keys	**A4, A4a,** B1	**A4, A4a**		**A4, A4a**		22
		St. Thomas, USVI	A4, A4a, B1	A4, A4a, C1		C1		22
	Porites spp.	GBR		**C15**, C28, C60	**C15, C131**	**C131**	**C15, C131**	1
	Porites spp.	Central Red Sea	**C15, D1a**	**C15, D1a**	**C15, D1a**	**C15, D1a**		6
Antipatharian corals								
Antipathidae	*Cirrhipathes* cf. *anguina*	Hawaii		C21_b1, C26_b1, C26_b2, C26_b3 (11–30 m)	C21_b1, C26_b1, C26_b2, C26_b3			23
	Antipathes griggi	Hawaii			C21_b1, C26_b1, D1a (24 m)			23
	A. grandis	Hawaii				C21_b1, C26_b1, C26_ b3 (34–91 m)	C21_b1, C26_b1, C26_ b3 (34–91 m)	23
	Stichopathes cf. *echinulata*	Hawaii					C15, C21_b1, C26_b1, C26_b2, C26_b3 (129 m)	23
	Stichopathes sp.	Hawaii and Johnston atoll					C21_b1, C31, C26_b1, C26_b2, C26_b3, D1a (182–396 m)	23

(continued)

Table 30.2 (continued)

			Depth (m)					
Family	Coral species	Location	Shallow (0–10)	Mid (10–20)	Deep (20–30)	Upper mesophotic (30–60)	Lower mesophotic (60–200)	Reference
Aphanipathidae	*Aphanipathes* sp.	Hawaii					C15, C21_b1, C26_b1, C26_b2, C26_b3 (88–127 m)	23
Myriopathidae	*Acanthopathes undulata*	Hawaii					C26_b1, C26_b2 (259 m)	23
	Myriopathes ulex	Hawaii					C15 (96 m)	23
	Myriopathes sp.	Hawaii and Johnston atoll					C15 (396 m)	23
Schizopathidae	*Bathypathes* sp.	Hawaii					C26_b3 (320 m)	23

GBR Great Barrier Reef, Australia, *GOE/A* Gulf of Eilat/Aqaba, *PR* Puerto Rico, *USVI* United States Virgin Islands, *FGB GOM* Flower Garden Banks National Marine Sanctuary, Gulf of Mexico

N = novel sequence. In the revised systematics of Symbiodiniaceae, Clade A = genus *Symbiodinium*; Clade B = genus *Breviolum*; Clade C = genus *Cladocopium*; Clade D = genus *Durusdinium* (LaJeunesse et al. 2018)

References cited in table: [1]Bongaerts et al. (2011) and references within; [2]Bongaerts et al. (2013), [3]Lucas et al. (2016), [4]Bongaerts et al. (2015b), [5]Bongaerts et al. (2015a), [6]Ziegler et al. (2015), [7]Pochon et al. (2015), [8]Chan et al. (2009), [9]Frade et al. (2008), [10]Lesser et al. (2010), [11]Serrano et al. (2014), [12]Polinski (2016), [13]van Oppen et al. (2011) , [14]Cooper et al. (2011), [15]Sinniger et al. (2017), [16]Nir et al. (2011), [17]Einbinder et al. (2016), [18]Byler et al. (2013), [19]Winters et al. (2009), [20]Daniel (2006), [21]Nir et al. (2014), [22]Serrano et al. (2016), [23]Wagner et al. (2010)

30.4 Symbiodiniaceae Genetic Diversity in Coral Hosts: From Shallow to Mesophotic Coral Ecosystems

From shallow to mesophotic coral ecosystems, environmental parameters such as light and temperature vary (reviewed in Kahng et al. 2019). These environmental parameters can lead to modifications in the host (e.g., in whole colony morphology and skeletal structure) and/or modifications in the Symbiodiniaceae (e.g., Symbiodiniaceae density and pigment concentrations) (Fricke and Schuhmacher 1983; reviewed in Kahng et al. 2019). Along a depth gradient, organisms hosting Symbiodiniaceae exhibit three scenarios pertaining to holobiont genetics: (1) the holobiont occurs only in specific depths, for example, the scleractinian coral *Acropora palmata* (Baker et al. 1997), (2) the host-Symbiodiniaceae genotypic combination is the same throughout the depths sampled as seen in the coral *Madracis senaria* (Frade et al. 2008; Bongaerts et al. 2015a), or (3) the host-Symbiodiniaceae genotypic combination changes over depth such that certain Symbiodiniaceae occur at shallow depths and other Symbiodiniaceae at deeper depths, with potentially an overlapping depth, like in the coral *Stylophora pistillata* (Table 30.2; Winters et al. 2009). In the third scenario, the underlying assumption is that, although the Symbiodiniaceae genotypes change with depth, the same host species occurs along the depth range. Sometimes, what was considered one host species with a wide depth distribution turns out to be several cryptic species (Schmidt-Roach et al. 2013). Barring such genetic evidence, some host species can inhabit shallow to mesophotic environments while hosting different Symbiodiniaceae.

Although the data available on Symbiodiniaceae genotypes in hosts from MCEs are far from exhaustive, several trends emerge (Table 30.2). The genus *Cladocopium* (formerly Clade C) dominates the corals inhabiting mesophotic depths (Table 30.2). The exceptions thus far are various species in the genus *Madracis*, which harbor Symbiodiniaceae from the genus *Breviolum* (formerly clade B, LaJeunesse et al. 2018), and *Porites* in which the genera *Symbiodinium*, *Breviolum* and *Cladocopium* (former clades A, B, and C, respectively) were found at mesophotic depths (Table 30.2). When a host species can host two Symbiodiniaceae genera such as *Durusdinium* (formerly clade D) and *Cladocopium,* or *Symbiodinium* and *Cladocopium*, the *Durusdinium* or *Symbiodinium* are often associated with the host individuals found up to 30 m, while the *Cladocopium* containing hosts occur at the deeper depths (Table 30.2). In these situations, some of the individual hosts may contain the Symbiodiniaceae genus common at a given depth and low levels of the Symbiodiniaceae found at the other depth (Byler et al. 2013). If environmental conditions change, there may be a shuffle of the proportions of the Symbiodiniaceae already found within the host (Mieog et al. 2007). This scenario, however, is in stark contrast to Symbiodiniaceae that are sometimes detected following a stressful event and/or with molecular techniques but are transitory and not part of the long-term symbiosis (LaJeunesse et al. 2009; McGinley et al. 2012; Lee et al. 2016). Within Symbiodiniaceae transitions also occur as a function of depth. For example, *Madracis formosa* and *M. pharensis* host *Breviolum endomadracis* (formerly *Symbiodinium* type B7, LaJeunesse et al. 2018) from shallow to upper mesophotic reefs, while *Breviolum* B15 (formerly type B15) occurs at detectable levels in these corals in mesophotic depths (Table 30.2).

30.5 Variation Between Symbiodiniaceae Genotypes: Facts vs. Extrapolation

In host species in which the holobiont genotypic composition changes over depth, the changes could potentially be attributed to Symbiodiniaceae properties. With the knowledge that genotypically different Symbiodiniaceae exist, studies comparing Symbiodiniaceae genotypes demonstrated that Symbiodiniaceae differ from one another in morphological, physiological, and ecological attributes (LaJeunesse et al. 2018). For instance, Symbiodiniaceae differ in cell size (LaJeunesse 2001). Symbiodiniaceae also exhibited significant differences in growth rates, chlorophyll levels, and their ratio to reaction centers, and Symbiodiniaceae that grouped according to these values did not mirror the clade-type affiliation (Hennige et al. 2009). Inorganic carbon acquisition (Brading et al. 2013) and photosynthetic carbon fixation (Leal et al. 2015) also varied between Symbiodiniaceae. In addition, the synthesis of mycosporine-like amino acids differed between Symbiodiniaceae within different genera (Banaszak et al. 2000), and gene transcripts from four enzymatic antioxidants were distinct between Symbiodiniaceae with greater variability in peroxidases compared to superoxide dismutases (Krueger et al. 2015).

The between Symbiodiniaceae differences manifest themselves into specific responses when Symbiodiniaceae encounter different environmental conditions. For example, when exposed to elevated seawater temperatures, the thylakoid membranes of Symbiodiniaceae dubbed "thermally tolerant" retained their stacking properties and ultrastructural integrity (Tchernov et al. 2004). On the other hand, the thylakoid membranes in Symbiodiniaceae referred to as "thermally sensitive" significantly and irreversibly altered their structure, reducing their photochemical energy conversion (Tchernov et al. 2004). Tchernov et al. (2004) focused on Symbiodiniaceae belonging to clades A, B, and C (now called the genera *Symbiodinium, Breviolum,* and *Cladocopium*, respectively) and found that thermally tolerant and sensitive Symbiodiniaceae co-occurred within the same clade, demonstrating a lack of a "characteristic cladal response" in the parameters measured. Likewise, elevated partial pressure of CO_2, as a proxy for ocean acidification, lowered the growth rate of *Symbiodinium* A13 and the photosynthesis of *Symbiodinium pilosum* (formerly *Symbiodinium* A2) but did not affect the measured parameters in *Symbiodinium microadriaticum* (formerly *Symbiodinium* A1) and *Breviolum* B1 (Brading et al. 2011).

Symbiodiniaceae physiological variability also occurs when two or more Symbiodiniaceae co-inhabit the same coral host. A recurring phenomenon emerges, whereby one of the Symbiodiniaceae genera appears to withstand certain environmental conditions better than the other, subsequently affecting the outcome for the entire holobiont. For example, the scleractinian coral *Pocillopora verrucosa* in Guam can host Symbiodiniaceae belonging to either the *Cladocopium* or *Durusdinium* genera (Rowan 2004). When exposed to 32 °C, the maximum quantum yield of photosystem II of the *Cladocopium* went down while that of *Durusdinium* went up. Following the return to ambient conditions, *Cladocopium* did not recover, exhibiting chronic photoinhibition (Rowan 2004). Likewise, the scleractinian coral *Acropora millepora* on the Great Barrier Reef (GBR) hosts *Cladocopium* and *Durusdinium* symbionts, and when these symbionts co-occur within the same coral colony, one of the genera numerically dominates over the other (Berkelmans and van Oppen 2006). *A. millepora* colonies from one site (Keppels), that hosted both *Cladocopium* and *Durusdinium*, changed the relative proportion of one genus over the other (shuffling) such that following transplantation and elevated temperature at Magnetic Island, the surviving colonies predominantly hosted *Durusdinium* (Berkelmans and van Oppen 2006). Based on these and other studies, some researchers extrapolated, referring to the "thermally tolerant symbiont lineage (*Symbiodinium* clade D)" (Stat et al. 2013) and as such, stated that corals with clade D, or after gaining clade D, will survive global climate change (Baker et al. 2004; Oliver and Palumbi 2009; Stat and Gates 2011; Stat et al. 2013). This generalization cannot be made since clade D (now the genus *Durusdinium*) includes multiple species, some of whom are highly host-specific (LaJeunesse et al. 2014).

Representatives of the genus *Durusdinium*, specifically *Durusdinium trenchii* (formerly called *Symbiodinium trenchii* or type D1a, LaJeunesse et al. 2014; LaJeunesse 2017), are not the only species and genus that can cope with environmental perturbations such as elevated temperature. In the same study in which *A. millepora* withstood the perturbation with *Durusdinium*, colonies from another site (Davies Reef), only hosted *Cladocopium* symbionts. Following transplantation to Magnetic Island, the *A. millepora* colonies that survived recovered from the thermal stress with their *Cladocopium* symbionts (Berkelmans and van Oppen 2006). Additionally, in a study on *S. pistillata* in the GBR, both the colonies sampled at 3 to 6 m and those from 15 to 18 m hosted only Symbiodiniaceae in the *Cladocopium* genus (Sampayo et al. 2008). But, colonies hosting *Cladocopium* C79 and C35/a exhibited lower survival rates compared to colonies harboring *Cladocopium* C78 and C8/a, which also possessed significantly more protein (Sampayo et al. 2008). Conversely, when the reaction of *S. pistillata* colonies hosting C1 or C8/a to an elevated temperature was compared to that of *Porites cylindrica* colonies hosting *Cladocopium* C15, the *P. cylindrica* colonies, with their C15 symbionts, were not as detrimentally affected by the thermal stress (Fitt et al. 2009). Likewise, in a comparison of *Cladocopium* C3 and C15 inhabiting different coral species in the GBR, the coral species hosting C15 withstood the elevated temperature better than the species hosting *Cladocopium* C3 (Fisher et al. 2012).

Symbiodiniaceae comparisons in octocorals also demonstrate that Symbiodiniaceae performance is context-dependent. The uncoupling of host-Symbiodiniaceae symbioses with a reduction in Symbiodiniaceae density and/or chlorophyll content is commonly referred to as coral bleaching (Glynn 1996). In the 2008 mass coral bleaching event in the GBR, Goulet et al. (2008) investigated octocoral species from 17 soft coral genera hosting Symbiodiniaceae within the *Cladocopium* genus, with a few species hosting either *Durusdinium* D3 or two Symbiodiniaceae within the *Breviolum* genus. The bleaching of some soft coral species over others, and the differential bleaching patterns within a colony, could not be explained by the Symbiodiniaceae within these soft corals (Goulet et al. 2008). The soft coral hosts with *Durusdinium* D3, for example, did not fare better than the other symbioses. Taken together, the attempt at ascribing physiological generalizations to Symbiodiniaceae genera and species within them relies on Symbiodiniaceae comparisons within the same and different hosts. These evaluations depend on the hosts and/or Symbiodiniaceae chosen for the comparisons and the conditions that are assessed. The conclusions, therefore, need to consider the context.

It is also imperative to keep in mind that the Symbiodiniaceae do not live in a void and that they are part of, and influenced by, the host and that different host-Symbiodiniaceae combinations exhibit different physiologies. For example, an experiment on the sea anemone *Exaiptasia pallida* (formerly called *Aiptasia pallida*) demonstrated that the oxygen fluxes of the holobionts, both at ambient and elevated temperatures, depended on the sea anemone-Symbiodiniaceae genotypic combinations (Goulet et al. 2005). *Exaiptasia pallida* originally from Florida with its *Symbiodinium sensu stricto* symbionts exhibited higher oxygen fluxes both at ambient and elevated temperatures compared to the *E. pallida* originally from Bermuda that hosted *Breviolum* (Goulet et al. 2005). An artificial symbiosis between *E. pallida* from Bermuda and *Symbiodinium* from Florida demonstrated a physiology that differed from either natal symbioses, with higher oxygen fluxes at elevated temperatures than the Bermuda *E. pallida* with Bermuda *Breviolum* (Goulet et al. 2005). Therefore, the same Symbiodiniaceae genotypes physiologically perform differently in different holobionts. Thus, although physiological and ecological trends in Symbiodiniaceae genotypes may occur, overarching generalizations may not be valid without taking into account the respective holobionts.

30.6 Symbiodiniaceae Genetic Diversity and the Deep Reef Refugia Hypothesis Revisited

With global climate change, shallow-water coral reefs experience frequent and recurring environmental perturbations leading to coral bleaching (Glynn 1996). If the Symbiodiniaceae population does not recuperate; coral bleaching can lead to the demise of the entire holobiont. Given that several Symbiodiniaceae hosting species occur both in shallow and mesophotic coral ecosystems, the deep reef refugia hypothesis entertains the possibility that mesophotic corals are more protected and stable and will act as a refuge, replenishing and revitalizing the depleted shallow-water coral communities (Glynn 1996).

Although optimistic, the deep reef refugia hypothesis may not apply to many host species harboring Symbiodiniaceae (Bongaerts et al. 2010a). First, MCEs experience disturbances (Bongaerts et al. 2013; Andradi-Brown et al. 2016; Appeldoorn et al. 2016; Smith et al. 2019) and therefore may not act as a refuge. Second, only about 25% of the coral species constituting coral diversity occur along a wide depth gradient (Bongaerts et al. 2010a). Hence, since the majority of holobionts do not occur on both mesophotic and non-mesophotic reefs, they may not be able to inhabit wider depth ranges. On Caribbean reefs, for example, some scleractinian corals occur only at shallow depths such as *Acropora palmata*, up to 6 m (Baker et al. 1997), and *Agaricia humilis* up to 10 m (Bongaerts et al. 2013). Conversely, the corals *Agaricia undata*, *A. grahamae*, and *A. fragilis* are not common shallower than 50 m (Appeldoorn et al. 2016). In the GOE/A, the octocoral *Scleronephthya lewinsohni* inhabits only mesophotic depths, and the octocoral species richness is higher in MCEs and differs from shallower reefs (Shoham and Benayahu 2017). The two octocorals that host Symbiodiniaceae and dominate the upper mesophotic zone, *Ovabunda* sp. and *Xenia* sp., are absent in the reef flat and upper fore-reef zone (Shoham and Benayahu 2017), although they are found in other non-mesophotic reef habitats (Gabay et al. 2013).

Lastly, if a host does occur along a broad depth range from shallow to MCEs, the host-Symbiodiniaceae genotypic combination may differ between depths. Either the host population and/or the Symbiodiniaceae genotypes may change over depth leading to different holobionts occupying different depths. Looking at the host, timing of reproduction, for example, may vary between depths such that reproductive isolation may occur (Shlesinger et al. 2018). In addition, lower host reproductive output in MCEs may dictate a limited contribution to reproduction in shallower environments (Shlesinger et al. 2018). Alongside reproductive differences over depth, different host populations may inhabit different depths, with sometimes host populations at the same depth, but on different reefs exhibiting more genetic similarities than host populations on the same reef, but between depths (Bongaerts et al. 2010b). Conversely in the Caribbean, population connectivity of the coral host *Agaricia lamarcki* (Fig. 30.1) occurred across sites and depths (Hammerman et al. 2018), but Symbiodiniaceae genotypes within this host exhibited depth zonation (Lucas et al. 2016).

Taken together, the holobiont genotypic composition may differ from shallow to mesophotic reefs, either due to host or Symbiodiniaceae population zonation. Host populations may not be able to mix between depths. From the Symbiodiniaceae perspective, if multiple Symbiodiniaceae co-occur in a host, their proportions may change (symbiont shuffling) with changing environmental conditions and/or depths. On the other hand, since many hosts associate with specific Symbiodiniaceae (Goulet 2006), these hosts may not be able to acquire exogenous Symbiodiniaceae that do not reside within that host species. Therefore, different holobionts as a function of depth within the same host species may potentially preclude MCE holobionts from successfully inhabiting shallower environments and vice versa.

30.7 Conclusions and Future Research Directions

An organism that harbors Symbiodiniaceae constitutes a holobiont, a host-Symbiodiniaceae genotypic combination that displays physiological and ecological traits that are more than the sum of its organismal parts. With growing access to, and interest in MCEs, knowledge on mesophotic organisms is growing, and the identification of these organisms is an integral and essential aspect to understanding them. If these organisms host Symbiodiniaceae, it is imperative to also identify the Symbiodiniaceae genotypes in order to comprehend the holobionts' ecology and physiology. Although some studies on MCEs incorporate Symbiodiniaceae identification (Table 30.2), many knowledge gaps exist. For example, surveys of MCEs identify numerous species of scleractinian corals and octocorals. Although many of these coral species harbor Symbiodiniaceae, the Symbiodiniaceae within these associations are not identified (Bridge et al. 2012b).

In addition, besides information on Symbiodiniaceae genotypes in some scleractinian corals and one publication on Symbiodiniaceae in black corals (Table 30.2), no data are available on Symbiodiniaceae in other cnidarians such as octocorals and sea anemones and other taxa, such as foraminiferans and sponges. This lack of knowledge is not due to the lack of hosts harboring Symbiodiniaceae in MCEs. In the GOE/A, the octocoral community in the upper mesophotic includes 20 octocoral species of which 16 species host Symbiodiniaceae (Shoham and Benayahu 2017). Furthermore, the two octocoral species numerically dominating the upper mesophotic, *Ovabunda* sp. and *Xenia* sp., host Symbiodiniaceae (Shoham and Benayahu 2017). Yet, despite the majority of octocorals and the abundant octocorals harboring Symbiodiniaceae, the Symbiodiniaceae genotypic identities within octocorals at mesophotic depths are unknown. Likewise, Symbiodiniaceae containing sea anemones, which also form mutualisms with anemone fish, were found in surveys of MCEs from the central GBR (Bridge et al. 2012a) and the GOE/A (Brokovich et al. 2008). Although these sea anemone species also inhabit shallower reefs, one cannot assume that the Symbiodiniaceae found in sea anemones at shallower depths are the same Symbiodiniaceae that inhabit mesophotic depths. Hence, Symbiodiniaceae identity is key in deciphering these symbioses, including understanding the holobionts' responses to environmental perturbations. Twenty-seven years after large-scale distinction between Symbiodiniaceae genotypes commenced, the importance of identifying Symbiodiniaceae is omnipresent, including its relevancy to MCEs.

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