Sponges

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Abstract

Sponges are dominant, but poorly understood, components of mesophotic coral ecosystems (MCEs). Herein, we review the current understanding of mesophotic reef sponges focusing on their biodiversity, ecology, and threats, and comparing this to shallow reef sponges. The few studies of MCEs report a large number of new species, for which their contribution to ecosystem services and our understanding of sponge biodiversity and evolution are unknown. Major threats to MCE sponges are similar to threats to deep-water sponge communities and to mesophotic corals: fishing activities, pollution, and climate change, as well as in the Caribbean, invasive lionfish predation on herbivorous fishes that can result in overgrowth of algae that smother corals and sponges. The current geographic, habitat, and sampling biases prevent a full understanding of mesophotic sponge biodiversity and their ecological roles. Future studies must include not only massive sponges, but also the rare and harder to collect encrusting sponges. It is premature to draw global patterns of diversity and distribution for mesophotic sponges, since MCEs have not been studied worldwide, and geomorphological features vary within regions, causing species distributions to be highly variable.

32.1 Introduction

Sponges (phylum Porifera) are dominant components of mesophotic coral ecosystems (MCEs) (Reed and Pomponi 1997; Slattery and Lesser 2012; Van Soest et al. 2014). MCEs are light-dependent ecosystems starting at 30–40 m and extending to over 150 m in tropical and subtropical regions (Hinderstein et al. 2010). Although sponges are assumed to play similar ecologic roles in MCEs as in shallow coral reefs (Diaz and Rützler 2001), their biodiversity, the ecosystem services they provide, and their socioeconomic value are unknown and remain critical knowledge gaps (Sinniger et al. 2016).

The physiological constraints of scuba and the high cost of submersible use have forced most sponge biologists to focus their research on shallow coral reefs (Slattery et al. 2011). In the 1800s and 1900s, deep-water sponge collections were made by dredging. Over the past 40 years, human occupied vehicles (HOV) or submersibles, remotely operated vehicles (ROV), and advanced technical diving have enabled better access to MCEs (Armstrong et al. 2019; Pyle 2019). Recent taxonomic sponge surveys at mesophotic depths using these technologies in the tropical western Atlantic (e.g., Van Soest et al. 2014) have revealed a surprising number of previously unknown taxa, further increasing the importance of studying these ecosystems as sources of ecological, physiological, and biochemical novelty.

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Herein, we review the current understanding of mesophotic reef sponges focusing on biodiversity, ecology, threats, and comparison to shallow reef sponges. We analyze the geographic extent of our knowledge, as well as current gaps in that knowledge, and the advantages and limitations of different technical approaches used to study these communities.

32.2 Biodiversity

To evaluate the status of knowledge of sponge biodiversity on MCEs, we first review what is known about sponge diversity from global, regional, and local studies. On a global scale, among the 12 ocean realms (Spalding et al. 2007), the total number of described Linnaean sponge species ranges from the lowest in the Arctic and Temperate Southern Realms (310 spp. each) to the highest in the Temperate Northern Atlantic (1664 spp.) and the Central Indo-Pacific (1325 spp.) (Van Soest et al. 2012). It should be noted, however, that these global diversity patterns likely reflect a sampling bias based on the restricted geographic range of collecting efforts, limited taxonomic training of local collectors, and the tendency to include mostly well-known species in published surveys (Van Soest et al. 2012). A recent study of sponges from the Pilbara region off western Australia in the Indo-West Pacific realm illustrates the importance of regional studies to accurately describe global patterns of biodiversity. Fromont et al. (2016) collated data on sponges from the Western Australian Museum and the Atlas of Living Australia that included both Linnean recognized species and operational taxonomic units (OTUs) or morphospecies. They listed 1164 sponge species, from depths of 10 to 5170 m, in a region where previous reports placed sponge biodiversity between 10 and 67 species (Van Soest et al. 2012). Of the 1164 species, 78% were endemic to one of the six bioregions studied, with only 12% widely distributed among all bioregions (Fromont et al. 2016). This disparity between what is known in terms of Porifera biodiversity on a global scale and what is discovered when a region is studied in greater detail is probably applicable for most areas of the world oceans.

Regional sponge biodiversity surveys of coral reef ecosystems have focused mostly on shallow habitats (<30 m) due to their ease of accessibility and to their relatively higher ecological value based on the extent of their well-known species richness. Since shallow coral reefs are areas where recreational, fishing, and tourism activities occur, they are also economically valuable. Moreover, these shallow communities are more likely to be affected by anthropogenic disturbances, making them more frequent targets of monitoring studies.

Caribbean shallow-water coral reefs are considered a biodiversity hotspot (Roberts et al. 2002). Sponges recorded from shallow coral reefs range from 80 to 236 species (Diaz

2011). However, the total number of accepted Caribbean species has been estimated to be greater than 800 (data extracted from Van Soest et al. 2017). Dozens of regional sponge studies and monographs have been published in the last century on Caribbean sponges, but less than a dozen studies have focused on the biodiversity of Caribbean mesophotic reef sponges (De Laubenfels 1934; Van Soest and Stentoft 1988; Lehnert and Van Soest 1996, 1999; Rützler et al. 2014; Van Soest et al. 2014; Van Soest 2017).

In the past 30 years, faunistic studies have also targeted deep sponge communities, driven mostly by the search for novel biomedical resources (Pomponi et al. 1996; Nakao and Fusetani 2010; Mehbub et al. 2014). Sponge biodiversity reported in these studies is also inherently biased as collections typically do not include encrusting or cryptic species and may not include the same species from different regions if their chemistry was well known.

32.2.1 Taxonomic Trends

The understudied status of MCEs is reflected in the fact that any taxonomic study of MCE fauna results in the discovery of new species. For example, in Jamaica, 19 new species of sponges (27% of the 70 species collected) were discovered using advanced technical diving between 70 and 117 m (Lehnert and Van Soest 1996, 1999). In general, regardless of the techniques used, tropical western Atlantic MCE collections that have undergone extensive taxonomic characterization have revealed between 27% and 42% new species (De Laubenfels 1934; Van Soest and Stentoft 1988; Rützler et al. 2014; Van Soest et al. 2014; Van Soest 2017). All sponge species reported in these studies are listed in Table 32.1, as well as other mesophotic species that have been reported from reviews of particular families or genera, such as Axinellida (Alvarez et al. 1998) and *Cinachyrella* (Rützler and Smith 1992). Table 32.1 documents most sponge species that have been found in MCEs from the tropical western Atlantic and is the basis for evaluation of taxonomic trends among mesophotic sponges. The list is not intended to be exhaustive, but rather a first look at the species reported in the literature. Research in progress by the authors suggests that species, depth ranges, and geographic distribution will increase as collections and locations are studied in greater detail.

A total of 241 species were recorded in mesophotic depths in the tropical western Atlantic, with 102 species (42%) also occurring in shallow water, 40 (17%) also occurring in deeper water (>150 m), 88 species (37%) occurring exclusively at mesophotic depths, and 11 species (5%) occurring at all three depth levels. The distribution of supraspecific taxa shows that certain genera have more species and are more abundant in MCEs in the Caribbean and Guyana including *Auletta* and *Phakellia* (Axinellida), *Acanthella*

Table 32.1 Sponge taxa reported during MCE surveys in the tropical western Atlantic (all species names updated using Van Soest et al. 2017)

Order	Family	Species	S	M	D	Z	Bar	Bra	Guy	SCC	GA	EA	FL-BAH	GM	Be	Atl	References
Class Homoscleromorpha																	
Homosclerophorida	Plakinidae	*Plakortis angulospiculatus* (Carter, 1879)	XX	XX		10–130			+	+	+	+	+		+		3
		Plakortis deweerdtaephila Vicente et al., 2016		X		32							+				27
		Plakortis insularis Moraes and Muricy, 2003	X	X		1–130		+	+								3
		Plakortis symbiotica Vicente et al., 2016		X		32											27
Class Demospongiae																	
Chondrosiida	Chondrosiidae	*Chondrosia collectrix* (Schmidt, 1870)	XXX	XX		1–76		+	+	+	+	+	+	+	+		1, 3, 7
Chondrillida	Chondrillidae	*Chondrilla caribensis* Rützler et al., 2007	XXX	XX		1–107		+	+	+	+	+	+	+	+		3, 15, 17
Verongiida	Aplysinidae	*Aiolochroia crassa* (Hyatt, 1875)	XXX	XX		5–100			+	+	+	+	+	+			3, 6, 28, 25,
		Aplysina bathyphila Maldonado and Young, 1998	X	XXX		85–114					+	+	+				16, 17
		Aplysina caissara Pinheiro & Hajdu, 2001	X	X		2–76		+	+								3
		Aplysina cauliformis (Carter, 1882)	XXX	X		3–100		+	+	+	+	+	+	+	+		3
		Aplysina ocracea Alcolado, 1984		XX		8–153				+							1, 15
	Pseudocera-tinidae	*Verongula* sp.		X		60–80				+	+	+					5, 6
		Verongula reiswigi Alcolado, 1984	X	X		15–80				+	+	+	+				5, 8, 28
	Ianthellidae	*Vansoestia caribensis* Diaz et al., 2015	X	X		15–100											3
Dendroceratida	Darwinellidae	*Chelonaplysilla americana* Van Soest, 2017	X	X		0.5–53			+	+	+	+	+	+			3
Dictyodendrillidae		*Igernella notabilis* (Duchassaing and Michelotti, 1864)	X	X		4–77			+	+	+	+	+				3
Dictyoceratida	Irciniidae	*Ircinia* cf. *dendroides* Schmidt, 1862		X		100–153	+					+					1
		Ircinia felix (Duchassaing and Michelotti, 1864)	X	X		1–100	+	+	+	+	+	+	+	+	+		1, 3
		Ircinia hummelincki Van Soest, 1978		X		100	+					+					30

(continued)

Table 32.1 (continued)

Order	Family	Species	S	M	D	Z	Bar	Bra	Guy	SCC	GA	EA	FL-BAH	GM	Be	Atl	References
		Ircinia strobilina (Lamarck, 1814)	XX	X		3–70		+	+	+	+	+	+	+	+		17, 25, 28
	Spongiidae	*Coscinoderma lanuga* De Laubenfels, 1936		X		79–80								+		+	29
		Hyattella cavernosa (Pallas, 1766)	X	X		1–73		+	+	+	+	+	+	+			17, 25
	Dysideidae	*Dysidea cf. etheria* (De Laubenfels, 1936)	XX	X		1–44											3
		Dysidea variabilis (Duchassaing and Michelotti, 1864)	X	X		>20 m							+	+	+		1,
		Euryspongia lankesteri Lehnert and Van Soest, 1999		X		79					+							17
	Thorectidae	*Smenospongia aurea* (Hyatt, 1877)	X	X		15–80		+	+	+	+	+	+	+			5, 10
		Smenospongia echina (De Laubenfels, 1934)	X	X		20–80				+	+						4, 5, 15
Haplosclerida	Callyspongiidae	*Callyspongia densasclera* Lehnert and Van Soest, 1999		X		91					+						17
		Callyspongia cf. pallida (Hechtel, 1965)	X	X		2–62		+			+						3
		Callyspongia plicifera (Lamarck, 1814)	X	X		5–64			+	+	+	+	+	+			17
		Callyspongia scutica Van Soest, 2017	X	XX		25–68			+								3
	Chalinidae	*Cladocroce guyanensis* Van Soest, 2017		X		100–130			+	+							3
		Haliclona aff. flagellifera (Ridley and Dendy, 1886)	X	X	X	20–410			+	+			+				3
		Haliclona cf. implexiformis (Hechtel, 1965)	XX	X		0.5–59			+	+	+	+	+	+			3
		Haliclona (G.) megasclera Lehnert and Van Soest, 1996		X		77				+							25
		Haliclona (H.) plakophila Vicente et al. 2016		X		32					+						27
		Haliclona (R.) strongylophora Van Soest and Lehnert, 1996		X		79–91					+						3
	Niphatidae	*Amphimedon caribica* (Pullitzer-Finalli, 1986)		X		76–85					+						17

Family	Species				Depth (m)								References
	Amphimedon nanaspiculata (Hartman, 1955)	X	X		12–71						+	+	3
	Niphates erecta Duchassaing and Michelotti, 1864	XX	X		1–94		+	+	+	+	+	+	17
	Niphates lutea Lehnert and Van Soest, 1999		X		82–85					+			17
Petrosiidae	Neopetrosia dutchi Van Soest et al., 2014		X		149						+		2, 6
	Neopetrosia eurystomata Van Soest et al., 2014		X		100–120	+			+	+	+		2
	Neopetrosia proxima (Duchassaing & Michelotti, 1864)	XXX	XX	X	1–156	+		+	+	+	+	+	1, 3, 25, 28
	Neopetrosia rosariensis (Zea and Rützler, 1983)	XX	XX		126–153	+			+	+	+		1
	Neopetrosia subtriangularis (Duchassaing, 1850)	XX	X		5–100			+	+	+	+	+	3
	Petrosia (S.) dendyi (Hechtel, 1969)	X	X		3–85				+	+			17
	Petrosia (S.) devoogdae Van Soest, 2017		X		104–130	+		+					3
	Petrosia (S.) hartmani (Van Soest, 1980)	XX	XX		10–100	+		+	+	+			1, 6, 34
	Petrosia (P.) massiva Lehnert and Van Soest, 1996		X		70					+	+		25
	Petrosia (P.) pellasarca (De Laubenfels, 1934)	X	XX		73–126	+			+	+	+		1, 4
	Petrosia (S.) stoneae (Van Soest and Stentoft, 1988)	X	XX	X	10–216	+			+	+			1, 6, 34
	Petrosia (P.) weinbergi Van Soest, 1980	X	X	X	10–184	+		+	+	+	+		3
	Xestospongia deweerdtae Lehnert and Van Soest, 1999	X	XX		8–82			+	+	+	+		17, 27
	Xestospongia muta (Schmidt, 1870)	XXXX	XXX		10–94				+	+	+		1, 3, 6, 28
	Xestospongia rampa (De Laubenfels, 1934)		XX		70–92				+	+			15, 25
Phloeodictyidae	Calyx podatypa (De Laubenfels 1934)	XX	X		2–100	+			+	+	+		1, 28

(continued)

Table 32.1 (continued)

Order	Family	Species	S	M	D	Z	Bar	Bra	Guy	SCC	GA	EA	FL-BAH	GM	Be	Atl	References
		Oceanapia ascidia (Schmidt, 1870)	X	X	X	10–270	+	+	+		+					+	3
		Oceanapia bartschi (De Laubenfels, 1934)	X	XX		5–91				+	+						17, 28
		Oceanapia carotta (Schmidt, 1870)		X		72–93	+	+	+	+	+	+	+				3
		Oceanapia oleracea (Schmidt, 1870)	X	X		2–45	+	+		+	+			+			22
		Oceanapia peltata (Schmidt, 1870)	X	X	X	3–216				+	+						1, 28
		Oceanapia cf. stalagmitica (Wiedenmayer, 1977)	X	X		8–66			+								3
		Oceanapia stalagmitica (Wiedenmayer, 1977)	X	X		8–70					+		+				31
		Siphonodictyon coralliphagum Rützler, 1971	XX	X		0.3–73		+		+	+	+					17, 25, 28
		Siphonodictyon densum (Schmidt, 1870)		X	X	130–216			+				+				3
		Siphonodictyon xamacayense (Pulitzer-Finali, 1986)	X	X		15–85				+	+	+					17, 25
Axinellida	Axinellidae	Auletta sycinularia (Schmidt, 1870)	X	X	X	70–200	+		+				+	+			1, 3
		Auletta tuberosa Alvarez et al., 1998		X		60–80			+	+		+	+	+			21, 6
		Axinella digitiformis Lehnert and Van Soest, 1996		X		71–88						+					17, 25
		Dragmaxia unduata (Alvarez et al., 1998)	X	XX		0.5–65			+	+			+				3, 21
		Phakellia folium Schmidt (1870)		XX	XX	70–600	+	+	+	+	+	+	+				1, 2, 3, 21
		Phakellia cf. connexiva Ridley & Dendy, 1887		X		>80		+				+	+	+			6, 21
		Phakellia bettinae Lehnert and Van Soest, 1999		XX		60–61					+						17
	Stelligeridae	Halicnemia sp.		X		100			+								3
		Higginsia coralloides Higgin, 1877	X	X		9–34	+	+	+	+	+	+	+	+	+		3
	Heteroxyidae	Didiscus oxeatus Hechtel, 1983	X	X		15–79					+	+	+				17
		Julavis jamaicensis Van Soest and Lehnert, 1997	X	X		20–106					+						17

Order	Family	Species				Depth (m)									References
		Myrmekioderma gyroderma (Alcolado, 1984)	XX	XX		15–110			+	+	+	+	+		1, 3, 4, 5, 26, 28
		Myrmekioderma rea (De Laubenfels, 1934)	XX	X		15–100	+	+	+	+	+				1, 3, 4, 26, 28
		Parahigginsia strongylifera Van Soest et al., 2014		X	X	100–238	+	+	+						2, 3
	Raspailiidae	*Aulospongus samariensis* Hooper et al., 1999	X	XX		6–90			+						3
		Ceratopsion rugosum (Schmidt, 1870)		X	XX	76–305				+					1, 21
		Raspailia (R.) johnhooperi Van Soest, 2017	X	X		27–44		+							3
		Raspailia (R.) tenuis Ridley and Dendy, 1886		X		<153	+								1
		Raspailia (P.) thamnopilosa Van Soest, 2017		X		96		+							3
		Thrinacophora funiformis Ridley and Dendy, 1886	X	X		12–81	+	+							3
Bubarida	Dictyonellidae	*Acanthella cubensis* (Alcolado, 1984)		XX		15–137			+				+		21
		Acanthella flagelliformis (Van Soest and Stentoft, 1988)		X	X	150–200	+								1
		Acanthella vaceleti Van Soest and Stentoft, 1988		X		65–108							+		1, 3, 21
		Dictyonella foliaformis Lehnert and Van Soest, 1996		XX		61–70				+					17, 25
	Desmanthidae	*Desmanthus incrustans* Topsent (1889)	X	X		12–80					+		+	+	6, 12, 14
		Petromica (C.) citrina Muricy et al., 2001	X	X		3–65	+	+							3
Scopalinida	Scopalinidae	*Scopalina ruetzleri* (Wiedenmayer, 1977)	XX	X		1–49	+	+	+	+	+	+	+		25, 32
		Stylissa caribica Lehnert and Van Soest, 1998		X		30–67				+					10
		Svenzea flava (Lehnert and van Soest, 1999)		X		76					+				17
Biemnida	Biemnidae	*Biemna cribaria* (Alcolado and Gotera, 1986)	X	X		60–91	+			+					1
		Biemna rhabdotylostylota Van Soest, 2017		X		64		+							3

Table 32.1 (continued)

Order	Family	Species	S	M	D	Z	Bar	Bra	Guy	SCC	GA	EA	FL-BAH	GM	Be	Atl	References
Tetractinellida	Ancorinidae	Asteropus albus (Alcolado & Gotera, 1986)		X		30											8
		Asteropus syringifer Van Soest and Stentoft, 1988		X		100	+										1
		Asteropus vasiformis Hajdu & Van Soest, 1992		X	X	150–153	+				+						1
		Rhabdastrella fibrosa Hechtel, 1983		X		27–98		+	+								3
		Stelletta cf. anancora (Sollas, 1886)		X		100	+	+							+	+	1
		Stelletta crassispicula (Sollas, 1886)		X		21–83		+	+							+	3
		Stelletta cf. gigas (Sollas, 1886)		X	X	100–153											1, 5
		Stelletta aff. pumex (Nardo, 1847)		X		100										+	1
		Stelletta vervoorti Van Soest, 2017		X		71–100	+		+								3
		Stelletinopsis megastylifera (Winterman-Killian and Killian, 1984)	XX	X		3–71			+	+		+		+			3
		Tribrachium schmidti Weltner, 1882	X	X	X	12–720		+	+		+						3
	Corallistidae	Corallistes paratypus Van Soest and Stentoft, 1988		XX	XX	>108				+							2
		Corallistes typus Schmidt, 1870		XXX	XXXX	>100	+	+	+	+				+		+	1, 2, 12, 13
		Neophrissospongia tubulata (Van Soest and Stentoft, 1988)		XX	XX	>108	+										1
	Geodiidae	Caminus carmabi Van Soest et al. 2014		XX		120–137				+							2
		Caminus sphaeroconia Sollas, 1886		XX		100	+	+				+					1
		Erylus alleni De Laubenfels, 1934		X		38–78											4
		Erylus bahamensis Pulitzer-Finali, 1986	X	X		>40											8
		Erylus clavatus Pulitzer-Finali, 1986	X	X		40–45											10
		Erylus geodiformis (Van Soest and Stentoft 1988)		XX	X	108–153	+										1
		Erylus goffrilleri Wiedenmayer, 1977	X	X		>40											7

Family	Species												
	Erylus incrustans Lehnert and Van Soest 1999		X		65–70	+		+					3
	Erylus rhabdocoronatus Van Soest, 2017		X		76	+		+					3
	Erylus surinamensis Van Soest, 2017		X		104–130	+							3
	Erylus transiens (Weltner, 1882)		XX	XXXX	100–1384							+	1
	Geodia corticostylifera Hajdu et al. 1982	X	X		30–82			+	+				25, 34
	Geodia gibberosa Lamarck, 1815	XXX	X		2–100	+		+	+	+	+		1, 3, 7
	Geodia pocillum Van Soest, 2017		X		96	+			+				3
	Geodia sulcata Van Soest, 2017		X		76	+			+				3
	Penares chelotropa Boury-Esnault, 1983		X		42–65		+						3
	Penares mastoidea (Schmidt, 1880)		X	XX	153–470			+	+				1
	Penares sineastra Van Soest, 2017		X		100	+			+				3
Pachastrellidae	*Characella aspera* (Sollas, 1886)		XX	X	108–153		+			+			1
	Characella enae (De Laubenfels, 1934)		X	X	153–366			+	+	+			1, 4
	Characella poecillastroides (Van Soest et al., 2014)		X	X	104–168	+		+					2, 3
	Pachastrella abyssi (Schmidt, 1870)		X	XX	108–>153					+	+	+	1, 2
	Pachastrella pacoi Van Soest et al., 2014		X	X	98–234								2, 3
	Poecillastra cf. *sollasi* (Topsent, 1890)		XX	XX	108–736					+	+	+	1
Neopeltidae	*Daedalopelta nodosa* (Schmidt, 1879)		X		142			+	+	+			2
	Neopelta perfecta Schmidt, 1880		X		119			+	+				2
Theonellidae	*Discodermia adhaerens* Van Soest et al., 2014	X	X		146				+	+			2
	Discodermia dissoluta (Schmidt, 1880)		X		10–89								28, 31
	Discodermia polydiscus Du Bocage, 1879		XX	X	100–153				+		+	+	1, 2

(continued)

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Table 32.1 (continued)

Order	Family	Species	S	M	D	Z	Bar	Bra	Guy	SCC	GA	EA	FL-BAH	GM	Be	Atl	References
		Racodiscula asteroides Zittel, 1878		XX	XX	>108	+				+	+		+			1, 12
		Theonella atlantica Van Soest and Stentoft, 1988		XX	XX	63–161	+		+	+				+			1, 2, 3, 4,6
	Thrombidae	*Thrombus kittoni* (Carter, 1874)		X		94–100	+		+	+							1, 3
	Theneidae	*Thenea muricata* (Bowerbank, 1858)		X	X	>100											1
	Siphonidiidae	*Gastrophanella implexa* Schmidt, 1879		XX	XX	140–153	+	+		+				+			1, 2, 12, 13
		Siphonidium ramosum (Schmidt, 1870)		X	XXX	104–439	+	+	+	+				+		+	1, 2, 3, 12, 13
	Scleritodermidae	*Aciculites higginsii* Schmidt, 1879		XX	XX	>108	+				+						1
		Amphibleptula madrepora Schmidt, 1879		XX	XX	>100	+				+						1
	Tetillidae	*Acanthotetilla gorgonosclera* van Soest, 1977	X	X	X	90–800	+					+	+				24
		Cinachyrella arenosa (Van Soest and Stentoft, 1988)	X	X	X	18–153	+					+					1, 11
		Cinachyrella kuekenthali Uliczka, 1929	XXX	X		<44 m	+			+	+	+	+	+			1, 6, 11
		Fangophilina submersa Schmidt, 1880		XX		42–101			+				+				3
		Tetilla pentatriaena Fernandez et al., 2011	X	XXX		19–81			+	+							3
Agelasida	Agelasidae	*Agelas clathrodes* (Schmidt, 1870)	XXX	XXX		10–153	+	+	+	+	+	+	+	+			1, 5, 6
		Agelas conifera (Schmidt, 1870)	XX	XX		10–102	+	+	+	+	+	+	+	+			17
		Agelas dispar Duchassaing and Michelotti, 1864	X	XX		76–104	+	+	+	+	+	+	+	+			17
		Agelas flabelliformis (Carter, 1883)		XX		60–110				+							2, 6
		Agelas sceptrum (Lamarck, 1815)	XXX	XXX		10–104	+	+	+	+	+	+	+	+			1, 17
		Agelas schmidti (Wilson, 1902)	X	XXX		1–144	+		+		+	+					1, 3, 17
		Agelas sventres Lehnert and Van Soest, 1996	X	XX		10–79					+	+	+				17, 26
		Agelas tubulata Lehnert and Van Soest, 1996	X	XX		12–91		+			+	+	+	+			17,26, 27

Order	Family	Species													Ref
	Astroscleridae	*Ceratoporella nicholsoni* (Hickson, 1911)	X	XX		22–79				+			+		17
		Hispidopetra miniana Hartman, 1969		X		76			+	+					13, 17
		Stromatospongia vermicola Hartman, 1969		X		76–88				+					17
	Hymerhabdiidae	*Hymerhabdia kobluki* Van Soest, 2017	X	X		24–94		+	+						3
		Prosuberites laughlini (Diaz et al., 1987)	XX	X		7–64		+	+						3
Polymastiida	Polymastiidae	*Polymastia agglutinans* Ridley and Dendy, 1886	X	X	X	15–800	+	+						+	3
		Polymastia fordei Lehnert and Van Soest, 1999		X		82				+					17
		Pseudotrachya amaza (De Laubenfels, 1934)	X	X	X	14–153	+	+	+	+	+			+	1, 3, 4
		Sphaerotylus bouryesnaultae Van Soest, 2017		X		93		+		+					3
Merliida	Hamacanthidae	*Hamacantha agassizi* Topsent, 1920	X	X	X	130–151	+	+					+		1, 3
Desmacellida	Desmacellidae	*Desmacella annexa* Schmidt, 1870	X	X	X	100–1280	+			+	+	+			1
		Desmacella polysigmata Van Soest, 1984	X	X		21–100	+		+		+				1
		Tylosigma ostreicola van Soest, 2017		X		64				+					3
Poecilosclerida	Acarnidae	*Acarnus* aff. *souriei* (Levi, 1952)		X		100	+	+	+	+					1
		Cornulum johnsoni (De Laubenfels, 1934)	X	X	X	1–720		+		+					3, 4
	Coelosphaeridae	*Coelosphaera (C.) hechteli* Van Soest, 1984		X		90				+					1
		Forcepia grandisigmata Van Soest, 1984		X		100			+	+					1
		Forcepia (F.) trilabis (Boury-Esnault, 1973)		X		100	+								1
		Forcepia (L.) vermicola Lehnert and Van Soest, 1996		X		88				+					31
		Lissodendoryx (L.) colombiensis Zea and Van Soest, 1986	XX	X		0.2–68	+	+	+	+	+				3

(continued)

Table 32.1 (continued)

Order	Family	Species	S	M	D	Z	Bar	Bra	Guy	SCC	GA	EA	FL-BAH	GM	Be	Atl	References
	Crambeidae	*Monanchora arbuscula* (Duchassaing and Michelotti, 1864)	XXXX	X		1–82	+	+	+	+	+	+	+	+			3, 17
	Crellidae	*Crella (P.) chelifera* Van Soest, 1984		X		90–101	+					+	+				1, 3
	Hymedesmiidae	*Hymedesmia (S.) alcoladoi* van Soest, 2017		X		64			+								3
		Hymedesmia caribica Lehnert and Van Soest, 1996		X		76					+						25
		Phorbas amaranthus Duchassaing and Michelotti, 1864	X	X		6–68		+	+	+	+	+	+	+			3
	Iotrochotidae	*Iotrochota agglomerata* Lehnert and Van Soest, 1999		XX		73–79					+						17
		Iotrochota birotulata (Higgin, 1877)	XXXX	XX		0.1–90			+	+	+	+	+	+			3
	Microcionidae	*Antho barbadensis* (Van Soest, 1984)		X		100	+										1
		Antho (A.) pellita Van Soest et al., 2014		X		108				+							3
		Antho (A.) penneyi (De Laubenfels, 1936)	X	X		2.5–81			+				+	+			3
		Clathria (A.) riosae Van Soest, 2017	X	X		25–88			+								3
		Clathria (C.) faviformis Lehnert and Van Soest, 1996		X		55											25
		Clathria (C.) gomezae Van Soest, 2017	X	X		25–120			+					+			3
		Clathria (M.) snelliusae Van Soest, 2017		X		34			+								3
		Clathria (T.) complanata Van Soest, 2017		X		81			+								3
		Clathria (T.) curacaoensis (Arndt, 1927)	XXXX	XX		3–71			+	+	+	+	+	+			3
		Clathria (T.) zeai Van Soest, 2017		X		67–68			+								3
		Echinochalina melana Van Soest and Stentoft, 1988		X		60–126	+										1

Order	Family	Species			Depth (m)										Ref
	Mycalidae	*Mycale (M.) arenaria* Hajdu and Desqueyroux-Faundez, 1994	X	X	3–59		+	+							1
		Mycale (M.) cf. laevis (Carter, 1882)	XXX	X	0–130			+	+						3
		Mycale (M.) quadripartita Boury-Esnault, 1973	X	X	23–80		+	+	+	+					3
		Mycale (Z.) angulosa (Duchassaing and Michelotti, 1864)	XX	X	1–58		+	+	+	+	+				3
	Myxillidae	*Hymenancora cristoboi* Van Soest, 2017		X	130			+							3
	Tedaniidae	*Tedania (T.) ignis* (Duchassaing and Michelotti, 1864)	XXX	X	0–91		+	+	+	+	+	+	+	+	3
		Tedania (S.) folium Van Soest, 2017		X	65			+							3
Clionaida	Clionaidae	*Cervicornia cuspidifera* (Lamarck, 1815)	X	X	4–65		+	+	+	+		+			3
		Diplastrella megastellata Hechtel, 1965	X	XX	1–91			+		+					25, 31
	Spirastrellidae	*Diplastrella spirastrelloides* Van Soest, 2017	X	X	94			+							3
		Spirastrella coccinea (Duchassaing and Michelotti, 1864)	XX	X	21–91		+	+	+	+	+	+	+	+	17
		Spirastrella erylicola Van Soest, 2017		X	76			+							3
Tethyida	Placospongiidae	*Placospongia ruetzleri* Van Soest, 2017	X	X	1–83		+	+	+			+			3
	Tethyidae	*Columnitis squamata* (Schmidt, 1870)	X	X	30–37			+	+				+		3
		Halicometes stellata (Schmidt, 1870)		X	81–650	X		+					+		3
		Hemiasterella camelus Van Soest, 2017		X	130			+							3
	Timeidae	*Timea tylasterina* Van Soest, 2017		X	81			+							3
Suberitida	Halichondriidae	*Axinyssa ambrosia* (De Laubenfels, 1936)	X	XX	18–85			+	+	+	+	+			3, 18
		Axinyssa yumae (Pulitzer-Finali, 1986)	X	XX	15–100	+		+	+	+	+				1, 18
		Ciocalypta alba Carvalho et al. 2003	X	X	12–71		+	+							3

(continued)

Table 32.1 (continued)

Order	Family	Species	S	M	D	Z	Bar	Bra	Guy	SCC	GA	EA	FL–BAH	GM	Be	Atl	References
		Epipolasis tubulata van Soest, 2017		X		67–68	+										3
		Hymeniacidon heliophila (Wilson, 1911)	XX	X		1–130		+	+		+	+	+	+	+	+	3
		Spongosorites ruetzleri (Van Soest and Stentoft, 1988)		XX	X	108–153	+			+		+	+				1, 2
		Spongosorites siliquaria Van Soest and Stentoft, 1988		XX	X	108–170	+				+	+					1,
		Topsentia bahamensis Diaz et al., 1993		X	XX	40–160				+	+		+				17, 19
		Topsentia ophirhaphidites (De Laubenfels, 1934)	XX	XX		1–130	+	+	+	+	+	+	+	+			1, 19
		Topsentia porrecta Topsent, 1928 = T. pseudoporrecta see below		X	XX	144–216											1
		Topsentia pseudoporrecta Diaz et al., 1993		X	XX	>140	+			+		+					2, 19
	Suberitidae	Aaptos aff. aaptos (Schmidt, 1864)		XX		100	+			+				+		+	1
		Aaptos pernucleata (Carter, 1870)	XX	X		0.5–40				+		+	+	+			7, 12
		Pseudospongosorites suberitoides (Diaz et al., 1993)	XX	X		0–88.5			+	+			+	+		+	3, 19
		Rhizaxinella clava (Schmidt, 1870)		X		130			+					+			3
		Suberites crispolobatus Van Soest, 2017		X		51–85											3
Class Hexactinellida																	
Lychniscosida	Diapleuridae	Scleroplegma lanterna (Schmidt, 1879)		X	X	120–200			+								3
	Dactylocalycidae	Dactylocalyx pumiceus Stutchbury, 1841		X	X	144–180		+		+	+						1, 2, 9
Sceptrulophora	Incerta sedis	Cyrtaulon sigsbeei (Schmidt, 1880)		X	X	108–170				+	+	+					1, 2
Class Calcarea																	
Clathrinida	Leucaltidae	Leucaltis clathria Haeckel, 1872	X	X		21–93		+	+				+		+	+	3
Leucosolenida	Leucosoleniidae	Leucosolenia salpinx Van Soest, 2017	X	X		27–39			+								3

Amphoriscidae	Amphoriscus ancora Van Soest, 2017		X	35	+	3
Grantiidae	Grantia kempfi Borojevic and Peixinho, 1976	X	X	19–71	+	3
	Leucandra aff. hentschelii Brøndsted, 1931	X	X	14–85	+	3

The relative abundance (X = rare, XX = common, and XXX = very common) at shallow (S = 0–30 m), mesophotic (M = 30–150 m) and deep habitats (D = >150 m), the depth range (Z) as reported in the referenced studies, their distribution in major Caribbean regions, and the references that report their mesophotic occurrence are presented.

Bar Barbados (1), *Bra* Brazil (13), *Guyana* Guy (3), *SCC* South and Central Caribbean (2, 7, 9, 15, 18, 23, 24, 27, 28, 30), *GA* Greater Antilles: Jamaica, Cuba, Puerto Rico, Cayman Islands (4, 5, 8,10, 17, 20, 21, 25, 27, 31), *EA* Eastern Antilles (1, 11, 14, 19, 26), *FL-BAH* Florida and Bahamas (5, 6, 7, 16, 21, 29, 33), *GM* Gulf of Mexico (5, 6, 11, 14, 16, 21, 22, 27), *Be* Bermuda (32), *Atl* Mediterranean, north eastern Atlantic, Carolinian, Guyana (1, 3)

1. Van Soest and Stentoft (1988); 2. Van Soest et al. (2014); 3. Van Soest (2017); 4. De Laubenfels (1934); 5. Slattery et al. (2017); 6. Reed et al. (2017); 7. Wiedenmayer (1977); 8. Alcolado and Gotera (1986); 9. Schulze (1887); 10. Lehnert and Van Soest (1998); 11. Ruetzler and Smith (1992); 12. Rützler et al. (2009); 13. Muricy et al. (2011); 14. Kobluk and Van Soest (1989); 15. Rützler et al. (2014); 16. Maldonado and Young (1998); 17. Lehnert and Van Soest (1999); 18. Zea et al. (2013); 19. Díaz et al. (1993); 20. Alcolado (1980); 21. Alvarez et al. (1998); 22. Schmidt (1870); 23. Zea (1987); 24. Van Soest (1977); 25. Lehnert and Van Soest (1996); 26. Pérez et al. (2017); 27. Vicente et al. (2016); 28. Díaz (2005); 29. De Laubenfels (1936); 30. Van Soest (1978); 31. Hechtel (1965); 32. Rützler (1986). 33. Pisera and Pomponi (2015); 34. Pomponi and Díaz, personal observation

(Bubaridae), *Halicnemia* (Stelligeridae), *Aulospongus* (Raspailiidae), *Penares* (Geodiidae), *Pachastrella* and *Characella* (Pachastrellidae), *Thrombus* (Thrombidae), *Siphonidium*, *Gastrophanella* and *Leiodermatium* (Siphonidiidae), *Scleritoderma* and *Aciculites* (Scleritodermidae), *Pseudotrachya* (Polymastiidae), *Coelosphaera* and *Forcepia* (Coelosphaeridae), *Desmanthus* and *Petromica* (Desmanthidae), *Antho* and *Echinochalina* (Microcionidae), *Phlyctaenopora* (Mycalidae), *Julavis* and *Parahigginsia* (Heteroxyidae), and *Topsentia* and *Spongosorites* (Halichondriidae). Most of these genera are not represented by species in shallow coral reef habitats in the tropical western Atlantic (Fig. 32.1).

The species in Table 32.1 represent 66 families (1 Homoscleromorpha, 3 Hexactinellida, 4 Calcarea, and 58 Demospongiae) and 24 orders (1 Homoscleromorpha, 2 Hexactinellida, 2 Calcarea, and 19 Demospongiae). This level of suprageneric diversity is high and similar to levels reported for mesophotic sponges from the Great Barrier Reef and Coral Sea deposited in the Queensland Museum, which are represented by 700 morphospecies from 73 families and 20 orders of Porifera (see Bridge et al. 2019).

In the Indo-West Pacific region, there have been fewer published taxonomic surveys of MCE sponges, however, there are important museum collections, for example, the collection of Indonesian sponges at the Naturalis Biodiversity Center (Leiden, The Netherlands), and the taxonomic reference samples made by the Coral Reef Research Foundation (Koror, Palau) for marine natural products research (deposited at the California Academy of Sciences, San Francisco, California, USA), from which biodiversity trends have been extrapolated herein.

A preliminary survey of 6000 museum sponge specimens collected from Indonesian reefs (housed at the Naturalis Biodiversity Center) indicates that diversity profiles of shallow (<40 m) and mesophotic (40–150 m) reefs in that region are generally similar to those observed in Caribbean reefs. The Indonesian MCE sponges share a species presence overlap of 56% with shallow-water reefs. Indonesian MCEs have distinctly higher species numbers of tetractinellid Demospongiae (especially lithistids) and Hexactinellida than shallow water (the latter are virtually absent there), while numbers of Calcarea, Keratosa, Verongimorpha, Clionaida and Poecilosclerida are significantly lower in MCEs than in shallow reefs. Other groups show similar diversity regardless of depth. A peculiar difference with Caribbean reefs is that lithistids in Indonesia are rather common in shallow water and are dominated by a few smaller non-habitat-forming species of the genus *Theonella* (notably *T. swinhoei*, which harbors rich populations of photosynthetic symbionts) (Van Soest, personal observation). Indonesian MCEs tend to have numerous larger habitat-forming lithistid species, for example, of the genera *Scleritoderma*, *Microscleroderma* and

Leiodermatium, probably similar to Caribbean MCEs (Pomponi et al. 2001; Pisera and Pomponi 2015), but with higher diversity.

Analysis of more than 2800 sponges collected by Coral Reef Research Foundation from Palau, Papua New Guinea, the Philippines, and Chuuk (Micronesia) reveal 178 species that occur deeper than 45 m (Bell and Kelly, personal observation) (Figs. 32.2 and 32.3). These sponges fall into two broad groups: (1) those that span shallow water down into mesophotic depths (69%) and (2) those that occur solely at mesophotic depths between 45 and 150 m (31%). Of the 178 species, 46% were found only in one locality and 10% were found in mesophotic depths in more than one location. Relatively few were found across the entire geographic area, but with more collection effort, this number might increase considerably. These 178 mesophotic sponge species represent 16 orders and 44 families. Species found across a broad depth range (15 to >70 m) include *Rhabdastrella globostellata*, *Hyrtios reticulatus*, *Theonella swinhoei* and two undescribed *Theonella* spp. Eight additional species were found only below 150 m. The latter were collected on submersible dives in Palau, and there are certainly more species to be found at those depths.

32.2.2 Survey Method Biases

When an MCE is surveyed using an ROV, much of the sponge fauna observed cannot be unequivocally identified without voucher specimens. During a recent exploration of Cuban MCEs, sponges were visually recorded from 30 to 150 m (Diaz and Busutil, personal observation). Approximately 25% of 296 species observed could only be characterized to the family, order or class level (Fig. 32.4). While it is often difficult to identify sponges with 100% certainty from photographs, photographic identification of shallow reef sponges typically yields much higher percentage identification to the species level (Schlacher et al. 2007; Diaz and Busutil, personal observation). The fact that one quarter of the sponges could only be identified to the family level, at best, suggests that these unidentifiable species may be restricted to MCEs and may be either poorly known or new species, or there could be different morphotypes on MCEs than on shallow reefs (i.e., phenotypic plasticity), which would be impossible to determine from photographs alone.

Studies of MCEs using HOVs have been more productive than ROVs in terms of visualizing and sampling unique species, although both are more expensive than advanced technical diving. Thirteen of the 31 specimens collected during four HOV dives on a Bonaire MCE were new species (Van Soest et al. 2014). The use of advanced technical diving has enabled collection of sponges with morphologies that are difficult to collect using an HOV or ROV manipulator (e.g.,
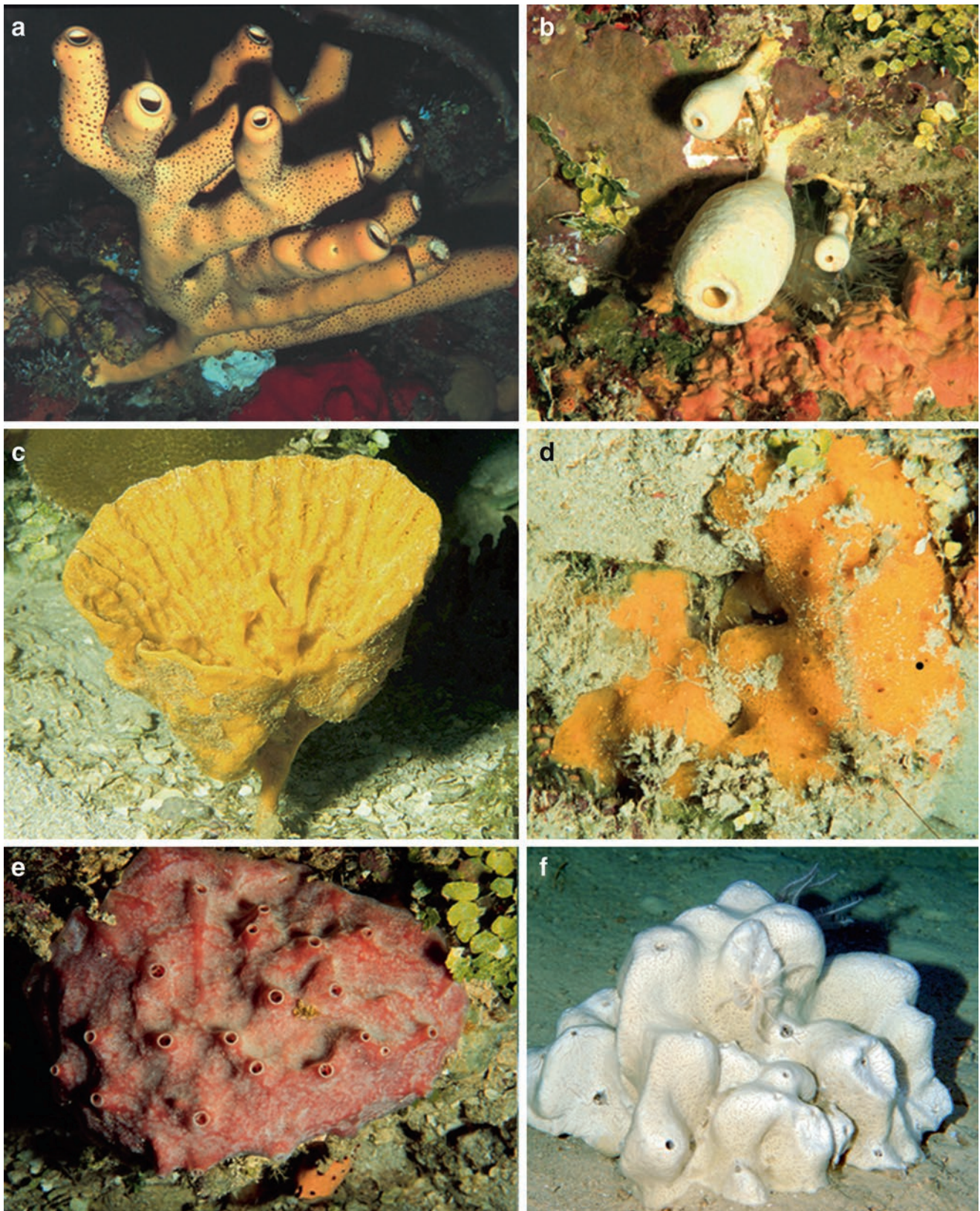
Fig. 32.1 Sponges from Caribbean MCEs: (**a**) *Agelas tubulata* (Agelasidae), Discovery Bay, Jamaica, 84 m. (**b**) *Aplysina bathyphila* (Aplysinidae), Discovery Bay Jamaica, 85 m. (**c**) *Dictyonella foliaformis* (Dictyonellidae), Discovery Bay, Jamaica, 61 m. (**d**) *Iotrochota agglomerata* (Iothrochotidae), Discovery Bay, Jamaica, 73–76 m. (**e**) *Xestospongia deweerdtae* (Petrosiidae), Discovery Bay, 76–82 m. (**f**) *Neopetrosia dutchi* (Petrosiidae) Bonaire, 149 m. (Photos: Helmut Lehnert: **a–e**; Van Soest et al. 2014: **f**)
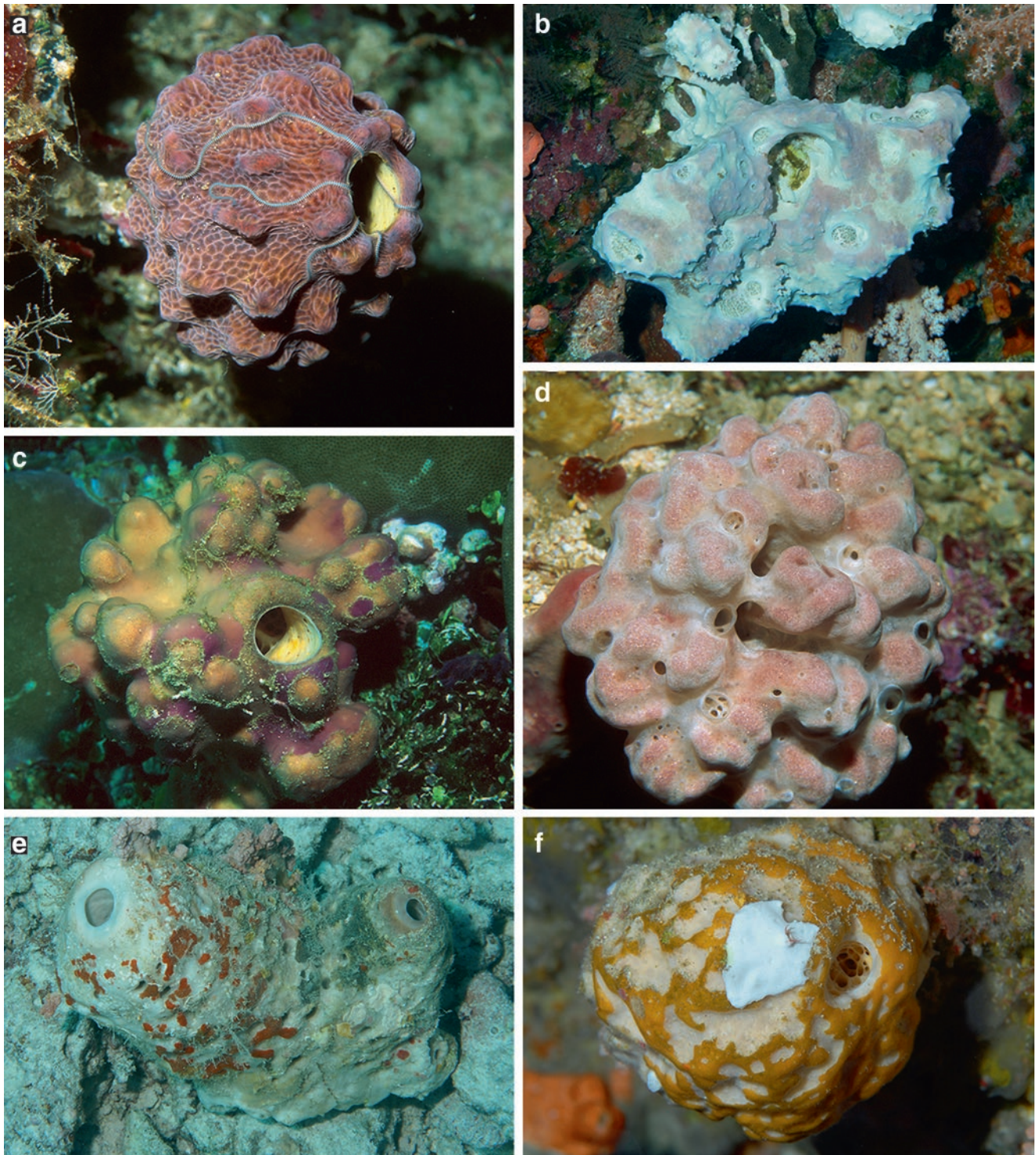
Fig. 32.2 Sponges from western Pacific MCEs: (**a**) *Suberea clavata* (Aplysinellidae), West Manus, Papua New Guinea, 46–52 m. (**b**) *Aplysinella* cf. *strongylata* (Aplysinellidae), Peleliu, Palau, 45 m. (**c**) *Rhabdastrella* sp. (Ancorinidae), West Manus, Papua New Guinea, 46 m. (**d**) *Coscinoderma* sp. (Spongiidae), New Hanover, Papua New Guinea, 60–68 m. (**e**) *Theonella cupola* (Theonellidae), Ulong Rock, Palau, 93 m. (**f**) *Theonella* sp. (Theonellidae), Kayangel, Palau, 70 m. (Photos: Coral Reef Research Foundation, Palau)
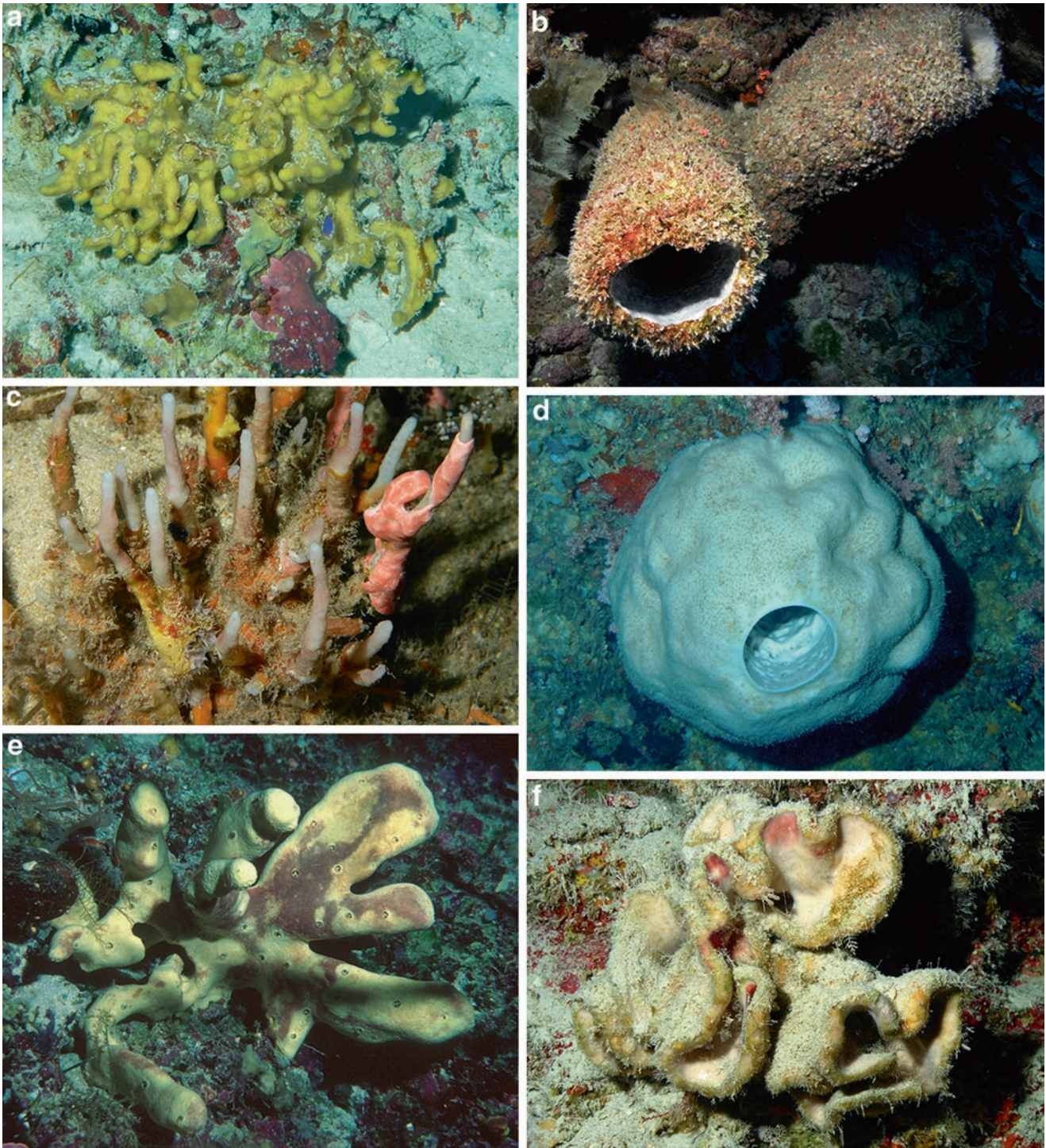
Fig. 32.3 Sponges from western Pacific MCEs: (**a**) *Rhabderemia sorokinae* (Rhabderemiidae), Uchelbeluu Reef, Palau, 74 m. (**b**) *Pachychalina* sp. (Niphatidae), Outer reef off Vangunu Island, Solomon Islands, 50 m. (**c**) *Oceanapia media* (Phloeodictyidae), West Babeldaob Inner Channel, Palau, 62 m. (**d**) *Theonella* sp. (Theonellidae), West Channel, Palau, 73 m. (**e**) *Hyrtios*. sp. (Thorectidae), Eastern Fields, Papua New Guinea, 65 m. (**f**) *Microscleroderma herdmani* (Scleritodermidae), Uchelbeluu Reef, Palau, 83 m. (Photos: Coral Reef Research Foundation, Palau)
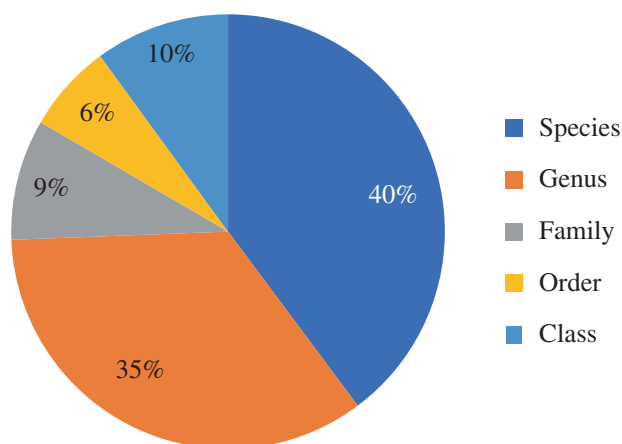
Fig. 32.4 Level of taxonomic identification of 296 distinct species observed during recent ROV dives on Cuban MCEs. (Busutil and Diaz, personal observation)

encrusting sponges) and from habitats that are not easily sampled by HOV or ROV (e.g., crevices, caverns, and vertical walls). The large number of new species (10 out of 27 collected) discovered by Lehnert and van Soest (1996) in 4 Trimix dives (60 min total diving time) supports this conclusion. Furthermore, detailed species distribution in those habitats can also be gathered when divers directly survey the substrate (see Sect. 32.3; Slattery and Lesser 2017).

32.3 Ecology

Few studies have discussed the relative abundance of MCE sponges. In the Mesoamerican Reef (Gress et al. 2019), sponges occupy from 1% to 39% of the substrate on MCEs, while in the Red Sea (Eyal et al. 2019) sponges occupy between 5% and 30%. The relative abundance of sponges is not only variable between MCE sites, but the relationship between sponge abundance in shallow vs. mesophotic depths also varies (see Gress et al. 2019). These studies suggest that sponge cover is variable and higher in some areas, such as Cozumel (Yucatan, Mexico) and one site in Utila (Honduras), but lower in others (another site in Utila) in comparison to shallow-water sponge cover (Gress et al. 2019). In the Bahamas and Cayman Islands, MCE sponge cover ranged from 60% to 80% cover at depths >60 m (Slattery and Lesser 2012); however, sponge cover has since declined due to competition with algae mediated by the lionfish trophic cascade (Lesser and Slattery 2011; Slattery and Lesser 2014).

Slattery et al. (2017) analyzed the species distribution and abundance (individuals m^{-2}) at five different depths across shallow and mesophotic reefs in the Bahamas and Little Cayman Island. Using advanced technical diving to survey and sample the MCEs, they recorded sponge diversity and abundance at 30, 45, 60, and 90 m and concluded that meso-

photic and shallow sponge diversity is different in the Caribbean. A distinct break in the sponge fauna occurs at ~60 m (with a transition zone at 30–45 m) and sponge assemblages from MCEs are more similar to one another than assemblages from shallow and mesophotic reefs at the same biogeographic location (Slattery and Lesser 2017; Slattery et al. 2017). Of the 98 species of sponges recorded, 42 were either exclusively found at >60 m in depth, or were represented by four times more individuals at the deeper mesophotic depths (60, 75, and 90 m) than in the shallower depths (3, 10, 20 m). Demosponge species from the orders Agelasida (*Agelas*), Axinellida (*Axinella*, *Phakellia*, and *Dragmacidon*), and Tetractinellida (*Geodia*, *Penares*, and *Cinachyrella*), and all Calcarea species observed were predominantly in these deeper mesophotic habitats. Certain species, including *Aplysina* (*A. bathyphila* and *A. lacunosa*), *Ceratoporella nicholsoni*, *Topsentia ophiraphidites*, *Callyspongia densasclera*, *Spirastrella coccinea*, *Clathria* spp., and *Myrmekioderma gyroderma*, also occurred in this deeper mesophotic habitat. In contrast, all recorded species of *Cliona* (*C. caribbaea*, *C. delitrix*, and *C. tenuis*) and *Niphates* (*N. digitalis*, *N. erecta*, and *N. erecta f. amorpha*), two species of *Callyspongia* (*C. armigera* and *C. vaginalis*), three species of *Aplysina* (*A. cauliformis, A. fistularis,* and *A. fulva*), *Erylus formosus*, and *Ectyoplasia ferox* were either exclusively or predominantly at <45 m in depth.

32.3.1 Symbioses

Marine sponges often contain dense and diverse microbial communities, which can constitute up to 35% of the sponge biomass (Taylor et al. 2007; Hentschel et al. 2012). Little commonality in microbial species composition or structure has been found across the phylum (Thomas et al. 2016). Sponge holobionts (containing photosynthetic and/or non-photosynthetic endosymbiotic bacteria) form the basis for the central roles that sponges have on global carbon (both dissolved and particulate organic carbon), dissolved organic nitrogen, and possibly phosphorous cycling (Wilkinson and Cheshire 1990; Diaz and Rützler 2001; de Goeij et al. 2013; Morrow et al. 2015; Zhang et al. 2015).

Phototrophic sponges (sponges with a photosynthesis respiration ratio >3) are important inhabitants in shallow tropical coral reefs (Wilkinson and Cheshire 1990; Erwin and Thacker 2007, 2008). Approximately 30% of common shallow reef species in Bocas del Toro, Panama, were found to harbor cyanobacterial endosymbionts (Erwin and Thacker 2007, 2008; Thacker et al. 2007). Several sponge genera known in shallow water to harbor cyanobacterial endosymbionts (Rützler 1990) also contain species present at mesophotic depths (e.g., *Ircinia* spp., *Aplysina* spp., *Petrosia* spp., *Neopetrosia* spp., *Erylus* spp., and *Geodia* spp.). The most

widespread type of association between cyanobacteria and tropical sponges is with the unicellular cyanobacterium *Synechococcus spongiarium*, which has been found to represent an extensive "cryptic diversity," with 15 distinct phylogenetic clades, determined by host identity and geography (Erwin and Thacker 2008). The relative abundance and importance of these sponge-microbial symbiotic systems in MCEs is unknown.

Van Soest et al. (2014) compared the biodiversity of sponges from shallow (<100 m) and deep water (>100 m) habitats in Bonaire. Distinct patterns of distribution and abundance were found among various Porifera taxa. For example, species bearing photosynthetic endosymbionts, such as taxa from the orders Dictyoceratida, Verongiida, Clionaida (family Clionaidae), and Haplosclerida (family Petrosiidae) have higher species richness on shallower reefs (<45 m), whereas, on the Great Barrier Reef, verongiids and other sponges with photosynthetic symbionts increased in abundance at mesophotic depths (see Bridge et al. 2019). However, several MCE surveys report an abundance of sponges hosting cyanobacterial symbionts (e.g., in the Caribbean: *Cribrochalina vasculum*, petrosiids, *Aplysina* spp., *Verongula* spp., and *Geodia* spp., and in the Great Barrier Reef: *Carteriospongia*), suggesting that there might be adaptations particular to deeper photosynthetic symbioses.

The coral *Montastraea cavernosa* and its photosynthetic dinoflagellate symbiont *Symbiodinium* demonstrate evidence of adaptation to depth in the Bahamas and the Gulf of Mexico MCEs. The photosynthetic symbionts were more abundant, unique, and had higher chlorophyll content at greater depths (Lesser et al. 2010). The existence of any particular adaptation or phylogenetic diversity of sponge-dinoflagellate symbioses at mesophotic depths remains to be investigated.

Due to decreased ability to conduct photosynthesis at mesophotic depths, it is possible that some sponges may shift towards heterotrophy on MCEs. A pattern of higher growth rates and larger sizes has been demonstrated in various studies (Pomponi et al. 1996; Lesser 2006; Slattery and Lesser 2012; Lesser and Slattery 2013). Transplant experiments have shown that deeper habitats are more conducive to higher sponge growth rates than in shallow habitats (Trussell et al. 2006). This could be the result of increased nutrient and particulate food abundance on Caribbean MCEs, as has been demonstrated for three Caribbean sponge species (Lesser and Slattery 2013; Slattery and Lesser 2015).

32.3.2 Ecosystem Function

Slattery and Lesser (2012) compare the relative abundance of major benthic groups between Caribbean (Bahamas and Cayman Islands) and Pacific (Chuuk and Palau) sites. They note that percent cover may have limited value in assessing sponge functional roles since cover was similar, but biomass on Caribbean reefs exceeds that of Pacific reefs by orders of magnitude. Thus, sponges may constitute a much more important functional component (in terms of biomass and nitrogen cycling) in Caribbean MCEs compared to Pacific sites.

Sponges contribute significantly to carbon, nitrogen, and silica cycling due to their high capacity for filter feeding (de Goeij et al. 2008, 2013; Maldonado et al. 2016). Most of the mesophotic sponges in the Pacific are thin encrusting sponges (e.g., *Spirastrella*). In Japan (see Sinniger et al. 2019), encrusting sponges dominate the MCEs studied, with massive sponges only occasionally found from 30 to 60 m. Competition between corals and encrusting sponges might be an important factor that contributes to community structure in this area.

Sponges provide habitat for fishes and invertebrates, including commercially important species (e.g., Knudby et al. 2013). The number and type of associated invertebrate macrofauna varies by sponge species (Sedberry et al. 2004). Sponges contribute to substrate modification on MCEs, both as bioeroders and as framework builders. Encrusting sponges may protect calcium carbonate substrates from bioeroders. Bioeroding sponges are the major long-term substrate modifiers in the 30–50 m depth range on a MCE in the U.S. Virgin Islands (Weinstein et al. 2014). Schoenberg et al. (2017) present data demonstrating a bathymetric trend with respect to which taxa tend to bioerode by depth. Clionaids tended to bioerode at depths <100 m, while species of the genera *Spiroxya*, *Alectona*, *Delectona*, and small *Siphonodictyon* dominated depths >100 m. This may be related to the presence of photosynthetic *Symbiodinium* in some species of *Cliona*.

In some locations (e.g., Jamaica), sclerosponges (i.e., demosponges with both siliceous spicules and a basal calcium carbonate skeleton) can replace corals as framework builders (Lang et al. 1975). In Palau, vertical reef walls deeper than ~90 m have ubiquitous lithistid (or "rock") sponges, typified by *Microscleroderma herdmani* (Colin, personal observation). These rock sponges are from diverse taxonomic groups and form hard framework structure at depth, a role similar to the sclerosponges of Jamaica (Lang et al. 1975). Although various morphologies of lithistid demosponges (e.g., *Discodermia* spp. and *Theonella* spp.) occur in tropical western Atlantic MCEs (Pomponi et al. 2001; Pisera and Pomponi 2015), they are not framework builders, as they may be in some Indo-West Pacific MCEs (Colin 2016).

In terms of socioeconomic value, sponges and their associated microorganisms are the most prolific source of marine natural products with potential pharmaceutical applications (Nakao and Fusetani 2010).

32.4 Threats

The threats to mesophotic sponges are similar to the threats to deep-water sponges (Hogg et al. 2010) and to mesophotic corals and other sessile benthic invertebrates (Andradi-Brown et al. 2016). The largest threat is physical damage caused by bottom trawling and other bottom fishing activities that result in sponges being ripped off the bottom, broken up into smaller pieces that may not survive, and smothered from sediments that are resuspended as a result of trawling or dredging (Hogg et al. 2010). Other anthropogenic threats include pollution from oil spills, as well as from cleanup efforts after spills (e.g., dispersants), waste disposal and dumping, and the placement of cables and pipelines (Hogg et al. 2010).

Large phase shifts on shallow mesophotic zones from coral- and sponge-dominated reefs to algal-dominated reefs have been well documented in the Bahamas (Lesser and Slattery 2011), caused by the decrease in herbivorous fish activity, due to predation pressure by lionfish population explosions, and to strong allelochemical competitive capabilities by algae such as *Lobophora variegata* (Slattery and Lesser 2014). Although sponge diseases or syndromes have rarely been reported from MCEs (Bongaerts et al. 2010), the Giant Barrel Sponge, *Xestospongia muta*, has been observed with a "wasting disease" at 60 m on the southern coast of Curacao (Slattery, personal observation).

It has been hypothesized that coral reefs may become sponge reefs as a result of lower pH and higher temperatures (Bell et al. 2013). Laboratory studies of shallow reef sponges (some of which also occur in MCEs) suggest that the warmer, more acidic conditions expected by the end of the century will have little effect on sponge ecology and physiology (Duckworth et al. 2012). However, lower pH and the weakening of coral skeletons may result in higher bioerosion rates by sponges (Duckworth and Peterson 2013; Wisshak et al. 2014).

32.5 Comparison to Shallow Reef Sponges

Analysis of the data in Table 32.1 suggests that most species reported from tropical Western Atlantic MCEs have restricted depth and/or habitat distributions: only 11 of the 241 species (5%) are present at all depth ranges. Of these, six (*Oceanapia ascidia*, *Oceanapia peltata*, *Tribrachium schmidti*, *Polymastia agglutinans*, *Pseudotrachya amaz*, and *Cinachyrella arenosa*) are adapted to soft bottom habitats. Therefore, their wider distribution is probably related to the existence of sandy or muddy patches in the localities studied.

The species that occur both in shallow and mesophotic reefs are spread among several sponge orders and families

(Table 32.1). However, all but one of the species of *Agelas* (family Agelasidae, order Agelasida) found in MCEs also occur on shallow reefs. Four of the five species of the class Calcarea reported from mesophotic depths also have a shallow reef distribution. On the other hand, no Hexactinellida taxa that occur on MCEs are found on shallow coral reefs. Within the demosponge order Tetractinellida, only four families (Ancorinidae, Geodiidae, Tetillidae, and Theonellidae) occur both on shallow and mesophotic coral reefs. Eighteen genera of nine other Tetractinellida families (Table 32.1) are abundant in MCEs and deeper reef areas (>150 m) and absent from shallow coral reefs.

A preliminary survey of Palau sponge fauna distributions (including the Southwest Islands) allows further comparison between MCEs and shallow reef sponges (Bell and Kelly, personal observation). From a total of 450 species recorded by the Coral Reef Research Foundation in Palau (based on museum specimens), 377 (84%) were found only in the shallow water zone (0–45 m), 42 (9%) were found only in the mesophotic zone (defined as 45–150 m), and just over 30 (7%) straddled both zones. These distribution data (19 orders, within 4 classes) illustrate some clear patterns (summarized in Table 32.2):

Table 32.2 Distribution of sponge higher taxa, across shallow (0–45 m) and mesophotic (45–150 m) zones of Palau coral reefs

Sponge taxa	Shallow zone % of 377 species	Mesophotic zone % of 74 species
Demospongiae		
Dictyoceratida	13.5	4.1
Lithistid Tetractinellida	0.5	17.6
Suberitida (= disused Halichondrida)	12.5	16.2
Haplosclerida	31.0	31.1
Poecilosclerida	15.6	8.1
Tetractinellida (Astrophorina)	3.4	5.4
Suberitida (formerly Hadromerida)	4.5	4.1
Agelasida	2.9	1.4
Verongiida	3.2	1.4
Dendroceratida	2.9	–
Chondrosiida	1.6	–
Chondrillida	0.5	–
Tetractinellida (Spirophorina)	1.6	–
Homoscleromorpha		
Homosclerophorida	2.4	5.4
Calcarea		
Clathrinida	2.9	–
Leucosolenida	0.8	1.4
Baerida	–	1.4
Lithonida	–	1.4
Hexactinellida		
Hexasterophora	–	1.4

- Dictyoceratida are as common in the shallow zone as they are in the tropical western Atlantic, but with a greater diversity of genera (*Luffariella* and *Dactylospongia* do not occur in the tropical western Atlantic) and species within those genera: *Coscinoderma*, *Spongia*, *Hyrtios, Hyattella*, *Luffariella*, *Ircinia*, and *Dactylospongia*.
- Lithistid Tetractinellida are diverse and common in the mesophotic zone (30–160 m). Common species are *Microscleroderma herdmani*, *Neophrissospongia microstylifer*, *Leiodermatium colini*, and *Costifer* sp.; and several species of *Aciculites*, *Theonella*, and *Siliquariaspongia* are highly speciose.
- Suberitida (= disused Halichondrida) are rare and spread more-or-less equally across shallow and mesophotic zones but are slightly more abundant in the latter.
- Haplosclerida are spread equally in the shallow and mesophotic zones, but are more common in the shallow water and across the boundary of the two zones (20–70 m). The shallow-water species are largely from families Chalinidae, Niphatidae, and Callyspongiidae, whereas Petrosiidae and Phloeodictyidae dominate deep mesophotic species.
- Poecilosclerida are more common in shallow water, particularly the families Microcionidae, Iotrochotidae, and Isodictyidae, but also occur in the mid-mesophotic (50–80 m).
- Tetractinellida (Astrophorina) are uncommon, but occur in the lower mesophotic zone (80–130 m; *Penares*, *Poecillastra*, and *Asteropus*), with the exception of the common shallow-water species *Rhabdastrella globostellata* that straddles the two zones.
- Tetractinellida (Spirophorina) are rare and restricted to relatively shallow water.
- Dendroceratida, Chondrosiida and Chondrillida are absent from the mesophotic zone.
- Homoscleromorpha (*Plakinastrella, Plakortis*) are relatively uncommon but appear in the mid-mesophotic zone (~40 to 70 m).

The highest species richness among Verongida, Dictyoceratida, Poecilosclerida, Agelasida, and certain Haplosclerida families (Niphatidae, Chalinidae, Callyspongiidae) in shallow coral reefs is shared both in tropical western Atlantic and Indo-Pacific reef systems. The high diversity and abundance of lithistid Tetractinellida and large Haplosclerida of the families Petrosiidae and Phloeodictyidae are reported from MCEs in both regions. However, tropical western Atlantic MCEs, at various locations, have abundant and highly diverse non-lithistid Tetractinellida (Astrophorina and Spirophorina) and abundant tubular and platey Verongiida. In both regions, there are few species of Homosclerophorida (Tables 32.1 and 32.2). However, the low number of Homosclerophorida reported for tropical western Atlantic MCEs is in contrast with the high number of recently described species from Jamaica shallow reefs (Ereskovsky et al. 2014) where 19 species of homocleromorphs were documented for the tropical western Atlantic. This study reached maximum depths of 28 m, so it is highly probable that observations and collections made using technical diving will extend the depth distribution of many shallow species of this enigmatic sponge class.

There are distinct mesophotic sponge supraspecific taxa that flourish in MCEs, but are absent or very rare in shallow coral reefs (Tables 32.1 and 32.2). Distinct suprageneric diversity is clear in MCEs from the tropical western Atlantic (Table 32.1). Nine Tetractinellida families and two Haplosclerida (Petrosiidae and Phloeodictyidae) are predominant and diverse in MCEs.

Few sponge species cover the entire range of shallow and mesophotic reefs (2% in the greater Caribbean); however, some of the very abundant shallow reef sponges such as *Xestospongia muta, Aplysina* spp.*, Agelas* spp., and *Geodia* spp. continue recruiting at upper and middle mesophotic depths. Those same genera appear deeper, but are represented by different species. Most of the abundant shallow MCE sponge species dwindle or disappear below 60 m. Slattery and Lesser (2017) suggested an important change in sponge species composition at this depth. The barrel sponge *Xestospongia testudinaria* occurs only on hard bottom slopes >50 m in Palau (see Colin and Lindfield 2019). Elsewhere in the Indo-West Pacific it is common in shallow-water reef areas (Bell et al. 2014). This is similar to the occurrence of the related species *Xestospongia muta* on shallow MCEs in the tropical western Atlantic (De Bakker et al. 2016).

32.6   Conclusion and Recommendations

A central discussion about MCEs is their importance as refuges for shallow coral reef flora and fauna. Our current knowledge of coral reef sponges indicates that there is an important percentage of the MCE sponge fauna that extends to shallow coral reefs (44% of MCE species in the western Atlantic and Caribbean; see Table 32.1), suggesting an important connectivity between these two ecosystems. The fact that most photosymbiont-carrying genera are conspicuous at MCEs also suggests that these associations might play an important role in this ecosystem.

Before an accurate comparison can be made between shallow and mesophotic reef sponges, more surveys and collections must be done in MCEs worldwide. The current geographic and habitat biases with respect to our understanding of MCEs prevent us from fully understanding the ecological roles of sponges in MCEs. Future collections must include not only massive sponges, but also the rare and harder to collect encrusting sponges.

Advanced technical diving and HOVs have been the best technologies to maximize the discovery of novel biodiversity with minimal environmental impact. ROVs are the preferred method to survey large areas, to discover and document the occurrence of MCEs, and to characterize the extent of sponge aggregations (area coverage and biomass) along major continental extensions. As with exploration of most environments, a nested approach should be applied to study these communities, starting with multibeam mapping to identify potential MCE sites, followed by ROV surveys, and continuing with more precise technical diving and HOV sampling. ROV surveys could also be used to monitor the state of MCE sponge fauna on a long-term basis. Technical diving and/or HOVs are the preferred methods to conduct in situ physiological and ecological experimentation.

The few studies of MCEs have revealed that there are a large number of sponge species new to science, of which diversity, evolutionary connections, and contribution to the ecosystem are unknown. The exploration of MCEs worldwide with a focus on MCE sponges remains a priority. Quantitative studies of MCE sponges remain a priority to better understand the scope of the ecological roles played by sponges in MCEs.

It is premature to draw global patterns of diversity and distribution (for example, depth limits for species) for MCE sponges, since large areas of the ocean remain unknown, and geomorphological features vary within regions, causing species distributions to be highly variable.

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