The Mesoamerican Reef

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Abstract

At over 1000 km in length, the Mesoamerican Reef (MAR) is a near-continuous reef system within four different countries: Mexico, Guatemala, Belize, and Honduras. MAR is the largest reef system in the Northern Hemisphere and is comprised of fringing and barrier reefs and offshore atolls, which extend into deeper water where mesophotic coral ecosystems (MCEs; 30–150 m depth) are found. Scientific studies of MCEs in the MAR began in the 1970s, and despite a rapid increase in marine research throughout the region in recent years, MCE ecological research has been restricted to a few locations and has been focused on hard (scleractinian) corals and fish communities. Hard corals have been documented at a maximum depth of 102 m in the MAR. However, hard corals do not represent the dominant benthic community at mesophotic depths in most cases. The benthic organisms providing structural habitat on many of the known MAR MCEs are octocorals, sponges, black corals, and calcareous macroalgae. Studies on MAR fish communities showed that a large proportion of fish species are found on both shallow reefs and MCEs. The limited data available suggests that MCEs are likely widespread along the MAR. There is evidence of the negative effects of fisheries, sedimentation, harvesting of black corals, and invasive lionfish on MAR MCEs. Improved identification and increase of biological and ecological studies of MCEs, coupled with an extension of scope to include mesophotic habitats in managed areas, should be undertaken to enhance their protection in the region.

Keywords

Mesophotic coral ecosystems · Mesoamerican Reef · Mexico · Belize · Honduras

5.1 Introduction

The Mesoamerican Reef (MAR) is a coral reef ecosystem approximately 1000 km long located on the western margin of the Caribbean Sea. It extends south from Cabo Catoche, Mexico, at the northern tip of the Yucatan Peninsula and runs along the coasts of Belize and Guatemala, before ending at the Bay Islands and fringing coastal reefs of Honduras (Fig. 5.1). The MAR is the largest reef system in the Northern Hemisphere and the second largest in the world, surpassed only by the Great Barrier Reef in Australia. The northern MAR consists of 300 km of fringing reefs along the east coast of the Yucatan Peninsula and extensive reefs around Cozumel Island and the Banco Chinchorro Atoll (Ardisson et al. 2011). The Belizean section at the center of the MAR spans approximately 250 km from Ambergris Caye to the Gulf of Honduras and encompasses a large barrier reef with hundreds of cays, along with three atolls seaward of the barrier reef (Turneffe Atoll, Glover's Reef, and Lighthouse Reef) (Rützler and Macintyre 1982). Guatemala has the shortest MAR coastline, only 150 km long, with large river outflows limiting reef development (Wilkinson 2008; Kramer et al. 2015). In Honduras, the MAR runs from east to west, with fringing reefs along the Honduran Caribbean north

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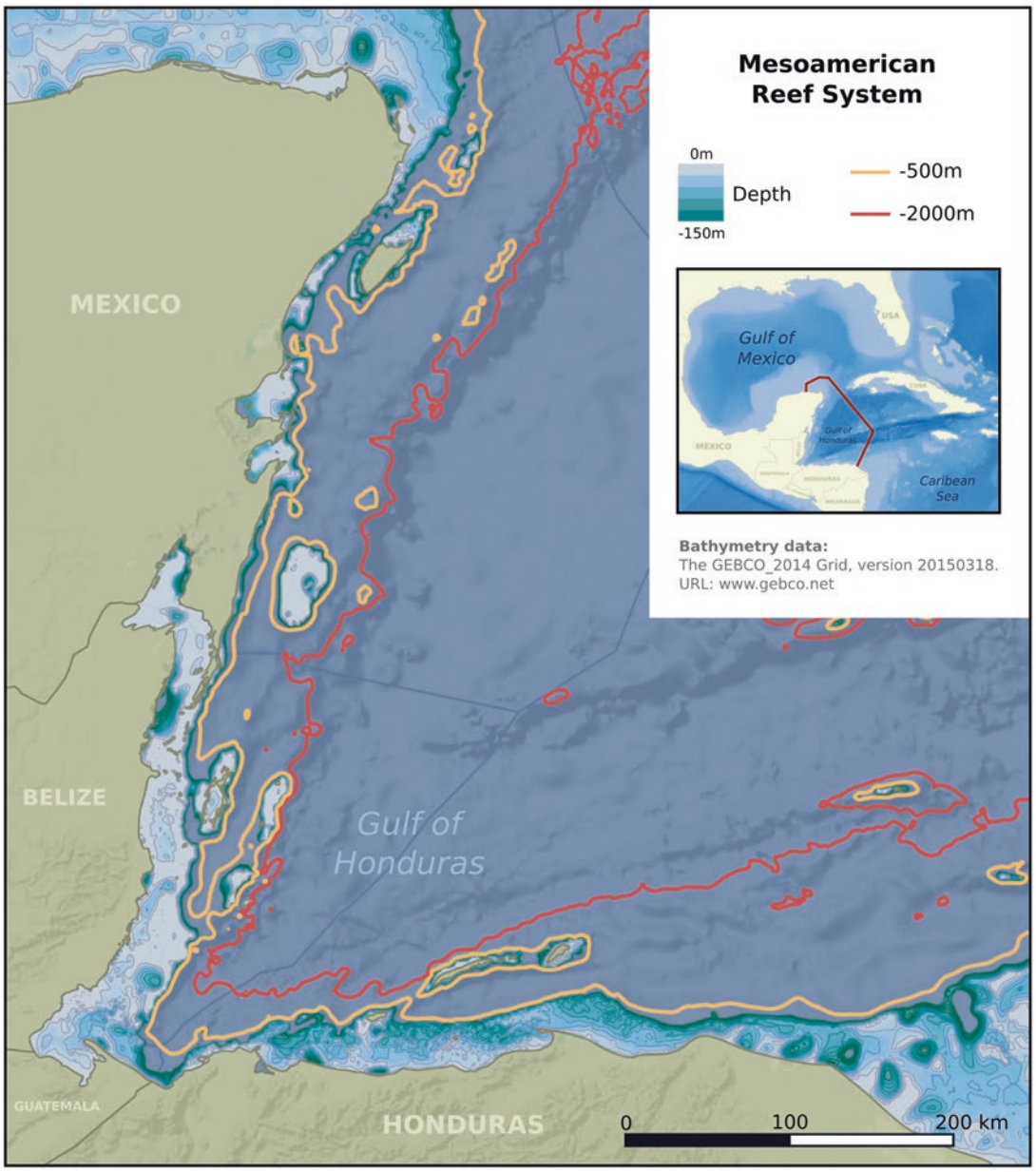

Fig. 5.1 Mesoamerican Reef (MAR) regional map. The red line on the inset map indicates the region shown in the main map

coast, and extensive reef dominated offshore banks. Reefs are also associated with continental shelf islands (e.g., Cayos Cochinos) and islands on the continental shelf edge (e.g., the Bay Islands of Roatan, Guanaja, and Utila).

The MAR region comprises a vast linked system of coastal habitats and is considered a biodiversity hotspot. The MAR has high ecological, aesthetic, and cultural and economic value while sustaining more than two million people from four countries (Chollett et al. 2017), making it an international conservation priority. In this chapter, we review the current state of knowledge of mesophotic coral ecosystems (MCEs; 30–150 m depth) in the MAR region.

5.1.1 Research History

The first MAR scientific cruises recording marine diversity began in the late nineteenth century. Hundreds of species, including corals and fishes from depths down to 3000 m, were described based on the collections by the US Coast Survey vessel *Blake* (1877–1880) expeditions. However, it wasn't until the 1970s that extensive taxonomic and ecological studies of MAR reefs began (Miloslavich et al. 2010). Observational studies using submersibles constitute the earliest modern qualitative analyses conducted on MAR MCEs (James and Ginsburg 1979). These early surveys often

reported the zonation of different taxonomic groups across a depth gradient and included interesting species-specific observations alongside more general reef geomorphology. The first dedicated MAR MCE biodiversity survey conducted was fish observations reported by Colin (1974), who recorded many unidentifiable fish species off Belize. In the 1990s, shallow-reef surveys began to extend into the upper-mesophotic zone (30–60 m), for example, in Roatan (Fenner 1993) and in Cayos Cochinos (Guzman 1998). Also at this time, in Cozumel, species-specific studies on black corals (Antipatharia) were conducted driven by harvesting pressures for the jewelry industry (Padilla and Lara 2003; Padilla Souza 2004). More recent work has used combinations of technical diving, remote camera drops, and submarines to survey detailed fish and benthic community structure on MCEs in Mexico (Gress et al. 2018) and Honduras (Andradi-Brown et al. 2016c, d; Gress et al. 2017; Laverick et al. 2017). Other recent work has considered biases in fish detection caused by survey technique choice on MCEs in Honduras (Andradi-Brown et al. 2016d, 2017a). Despite this growing body of MAR MCE research, investigations have been confined to a few locations, and no studies have addressed whether recorded biodiversity patterns are representative of the whole region.

5.2 Environmental Setting

Sedimentation is a major problem for the MAR as a whole, which is exposed to terrestrial runoff annually (Chérubin et al. 2008). MAR health is affected by the proximity to shore, and the levels of riverine and sediment input, caused by land clearance activities (Harborne et al. 2001). At the southern end of the MAR (Fig. 5.1), reefs are subject to twice-yearly pulses of terrestrial runoff, caused by both the initial runoff impact itself, but then also by this runoff being cycled in a gyre that returns the pollutants to the reefs several months later (Paris and Chérubin 2008). Off Guatemala, the most established and best-studied reefs are the carbonated banks of Punta Manabique, which are dominated by sediment-tolerant coral species, because of the high sediment input (Wilkinson 2008; Kramer et al. 2015). The coastline of the Yucatan Peninsula lacks terrestrial freshwater input from surface rivers, as its limestone structure results in an outflow of freshwater through underground river systems accessible through sinkholes (Spalding et al. 2001). Although it is not clear how this affects sedimentation rates on the northern MAR.

Other environmental parameters are poorly surveyed in the MAR. Currents in the region can be strong, especially in the north, with average speeds of 0.61 and 0.54 m s^{-1} at 35 m depth and 0.54 and 0.47 m s^{-1} at 105 m depth when measured at specific points in 2006 and 2007, respectively (Muhling et al. 2013). In Belize, on the reef off Carrie Cay in June, photosynthetically active radiation readings of 28.1 W m^{-2} and 17.1 W m^{-2} were recorded in 30 m and 39 m depths, respectively, compared to 86.6 W m^{-2} in 12 m (Shick et al. 1996).

Large-scale reef geomorphology changes across the MAR affect the habitat availability for MCEs in different parts of the region. On the northern MAR, the insular shelf area is narrow off the western coast of Cozumel, at around 500 m width, but wide, at 2000 m width, off the northern and eastern coast (Günther 1990; Muckelbauer 1990) (Fig. 5.2). For the central MAR, the continental side of the barrier reef is separated from the mainland by a lagoon which ranges from 15 to 50 km in width and extends to 65 m in depth (Purdy et al. 1975; Miller and Macintyre 1977; James and Ginsburg 1979). The central MAR also encompasses four atolls, which have steep exposed drop-offs that extend to submarine canyons and the Cayman Trench (Etnoyer et al. 2015). The southern MAR is composed of coastal fringing reefs, reef banks on the approximately 75-km-wide continental shelf, and a series of reefs associated with islands on the shelf edge (Harborne et al. 2001).

In Cozumel, three terraces can be found on the western shelf, at 5, 10, and 20 m depth, where the insular shelf edge begins (Muckelbauer 1990). On the eastern side, terraces have been observed at 3, 10, 20, 30, and 50 m depth. Below the western side terraces, the insular slope drops at an angle of 75–80° to a depth of 400 m, while on the eastern side, it drops near vertical to a depth of >1000 m (Muckelbauer 1990). In Belize, James and Ginsburg (1979) performed multiple submersible dives near Glover's Reef and Tobacco, South Water, and Queen Cays down to depths of 300 m. Through exploration of these reefs, James and Ginsburg (1979) described the morphology of two distinct styles of platform margins found in the central MAR: (i) reef to shallow basin and (ii) reef to oceanic trough. They found that reef margins near a shallow basin typically exhibited a steep transition below spur-and-groove structure down to a step at approximately 30–37 m depth, except near South Water Cay, where the step is absent. Continuing seaward from the base of the step, a sandy slope progressively transitions to the top of a wall. In some locations, they observed a break in the slope near 45 m (Fig. 5.2). Belizean mesophotic depths near oceanic troughs either have a similar profile to shallow basin reef sites or, for the east side of Glover's Reef, lack a distinct step and sandy slope. Instead, the east side of Glover's Reef has a convex brow at 25–60 m depth, where a vertical wall begins and extends >100 m depth. On the southeastern margin of Glover's Reef, the seaward portion of the reef exhibits a 45° slope, which terminates in a vertical wall at 30–40 m depth (Fig. 5.2).

In Honduras, on the south shore of Utila, the third largest Bay Island, shallow reefs form a spur-and-groove system, which transitions from a gentle reef slope to a flat seabed at

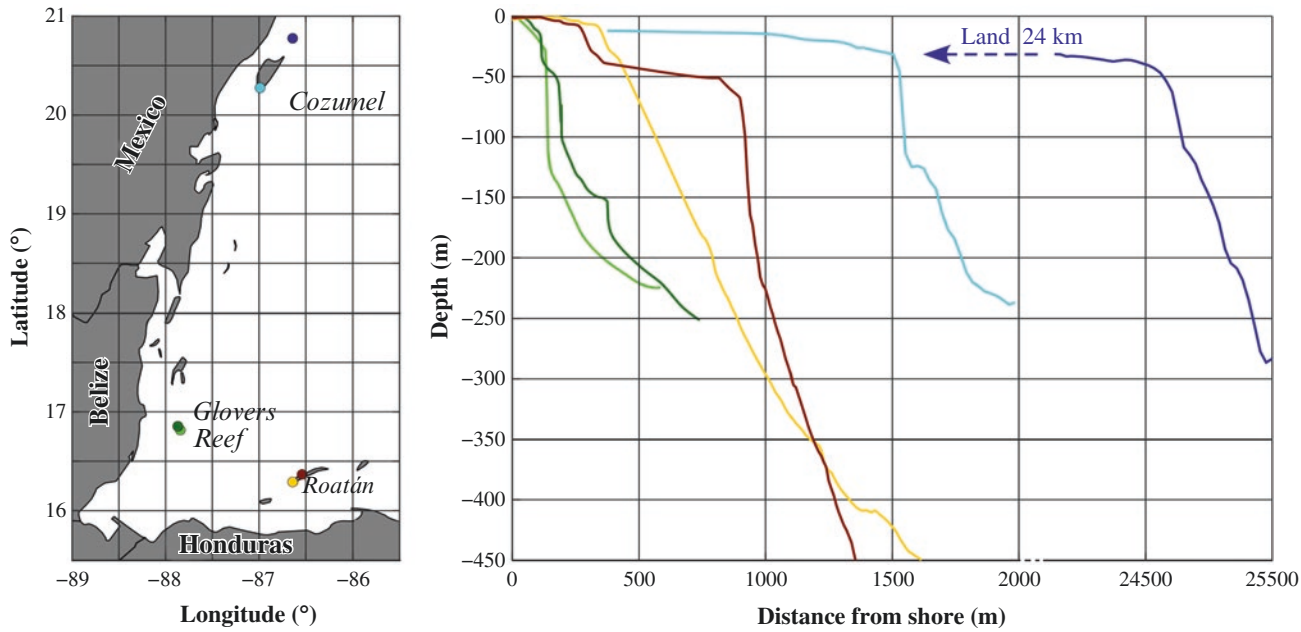

Fig. 5.2 Map and depth profiles across a shallow reef to MCE depth gradient for the MAR. The colors of the lines in the depth profiles match the colored dots in the map to indicate survey locations. Locations were southwest (red) and northwest (yellow) Roatan, northern (dark blue) and southern (light blue) Cozumel, and west (dark green) and southwest (light green) Glover's Reef. Cozumel profiles are derived from multibeam data from the Texas A&M University (http://gcoos.tamu.edu/products/topography/SRTM30PLUS.html) and from bathymetric mapping conducted in September 2016 by Jacobo Caamal from Comunidad y Biodiversidad A.C, Mexico. Glover's Reef profiles are redrawn from Figs. 3, 4, and 5 in James and Ginsburg (1979). Roatan profiles are derived from multibeam bathymetric mapping of the Roatan Peninsula conducted 9–10 July 2013 using Falkor's Kongsberg EM302 and EM 710 accessed via NOAA's National Geophysical Data Center (https://schmidtocean.org/serendipitous-side-trip). Roatan depths shallower than 40 m are taken from profiles redrawn from Mehrtens et al. (2001) and linear interpolation to the multibeam dataset

approximately 30–40 m depth (Andradi-Brown et al. 2016c). Off the north shore of Utila, there is an extensive platform at 6 m depth, with the reef dropping near-vertically from approximately 8 m to >100 m depth. Several terraces, approximately 20 m wide, have been observed to break this steep wall at depths of 30, 55, and 70 m (Andradi-Brown et al. 2016b). On Roatan, at the southwest end of the island, there is a shallow terrace from the island edge that gently slopes to approximately 10 m depth, where the edge of the continental shelf edge steeply drops (Mehrtens et al. 2001; Fig. 5.2). Off the northwest of the island, there is an extensive terrace approximately 500 m wide at a depth of 40–60 m (Fig. 5.2).

5.3 Habitat Description

Patterns in reef geomorphology affects the MCE communities found across the MAR at different depths. Many MCE communities are found far from land on large continental shelf areas. This includes on reef banks, such as off Honduras (Harborne et al. 2001), and also on extensive patch reef communities, which have been observed in the Belize Reef lagoon (James and Ginsburg 1979; Miller and Macintyre 1977). In some cases, coastal shallow fringing reefs, exhibiting spur-and-groove structures, transition into MCE patch reef communities. For example, off the south shore of Utila, patch reefs in the 35–60 m depth range vary in area between 1 and 500 m^2, and some raise to heights up to 3 m above the surrounding seabed (Fig. 5.3). These Utilian patch reefs share many species with the adjacent reef slope at 25–30 m depth (Andradi-Brown et al. 2016c). Shallow fringing reefs extend along most of the MAR coastline; however, little information on adjacent MCE communities is available.

On the steep walls associated with shelf edges, the most extensive MCEs have developed on terraces. For example, on the eastern side of Cozumel, the terraces at 30 and 50 m depth have hard coral (scleractinian) communities (Muckelbauer 1990), while off the north shore of Utila, extensive mesophotic hard coral communities have been recorded on terraces at depths of 30, 55, and 70 m (Andradi-Brown et al. 2016b; Laverick et al. 2017). Terraces, however, do not always contain well-developed MCEs. In northwest Roatan, the extended platform at 40–60 m depth is mainly covered with sand and a few scattered small MCE patch reefs, while at the terrace edge, MCEs are more extensive (Fig. 5.4b).

MCE communities can also form as continuous reefs across the depth gradient, for example, on the steep slopes on the western side of Cozumel (Gress et al. 2018) and in southwest Roatan (Fig. 5.4a). Steep slopes and walls rapidly reduce light levels available for benthic organisms (Brakel

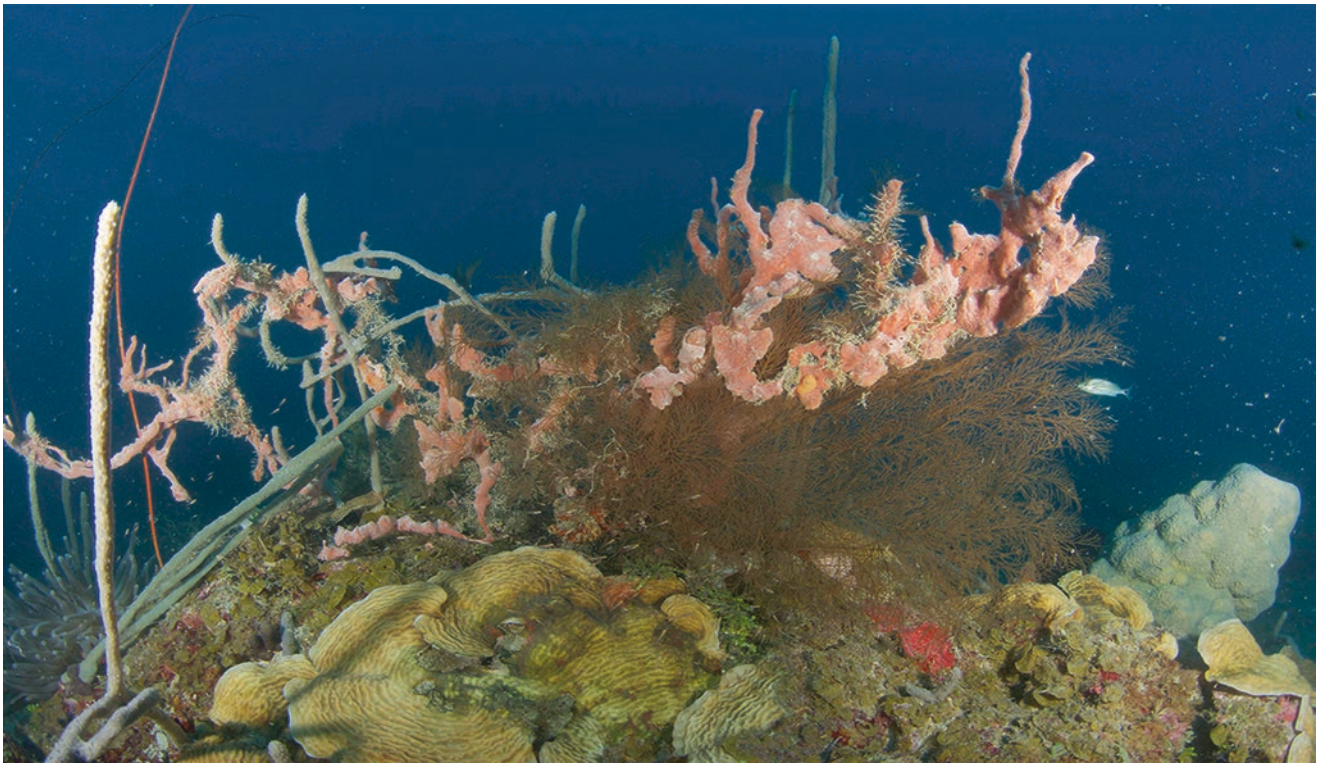

Fig. 5.3 Many MAR MCEs are dominated by sponges, calcareous macroalgae, black corals, and gorgonians as illustrated in this MCE patch reef approximately 60 m depth off the south coast of Utila, Honduras (Photo credit: Ally McDowell)

1979; Baker et al. 2016). Therefore, although hard corals are present, MCEs on steeper slopes and walls tend to be dominated by heterotrophic feeding organisms such as sponges, gorgonians, and black corals, which provide most of the structural habitat (Gress et al. 2018).

5.4 Biodiversity

5.4.1 Macroalgae

With the exception of a few locations, little is known about algal coverage on MCEs in the MAR. Macroalgal cover declines with depth on reefs around Utila, Honduras, for example, from 45% of benthic habitat cover at 15 m to 8% at 40 m (Andradi-Brown et al. 2016c), and is near-absent at 70 and 85 m (Laverick et al. 2017). However, this decline may be particularly severe on Utila because of the rapid decline in hard substrata availability for the majority of surveyed MCE communities (Andradi-Brown et al. 2016c). In contrast, in Cozumel, Mexico, macroalgae broadly increases in coverage between 15 and 55 m depth (Gress et al. 2018). For example, adjacent to tourist developments, fleshy and calcareous macroalgae increased from 5% and 12% at 15 m to 21% and 24% at 55 m, respectively. Within the Cozumel protected area, calcareous macroalgae increased from 22% at 15 m to 39% at 55 m, though fleshy macroalgae declined from 10% at 15 m to 5% at 55 m. Much of the increase in calcareous macroalgae with increased depth is driven by large areas of *Halimeda* spp. on MCEs (Gress et al. 2018). In Belize, *Halimeda* spp. commonly grow on sediment slopes and on rock surfaces to a depth of approximately 75 m. Below 75 m, *Halimeda* spp. are rare or absent, although a solitary deep attached specimen of the genus was observed at 110 m (James and Ginsburg 1979). Crustose coralline algae (CCA) are common on MCEs formed on vertical walls in Belize from 40 to 110 m. From 75 to 90 m, CCA covers an estimated 30–50% of the exposed benthos, and the deepest known CCA in the region was reported at 250 m (James and Ginsburg 1979).

The most detailed study of mesophotic macroalgae has been conducted on upper MCEs (30–60 m) in Belize. To assemble a list of marine plants found around Glover's Reef, Tsuda and Dawes (1974) collected specimens from six locations at 30–40 m depth. They recorded at least 15 species of green algae, 5 species of brown algae, and 8 species of red algae from mesophotic depths (Table 5.1). In addition, near Carrie Bow Cay, algae were collected from two seaward sites on the barrier reef at depths of 30–40 m (Norris and Bucher 1982). The most abundant algae found on the fore-reef slope of Carry Bow Cay to 40 m were *Lobophora variegata*, *Stypopodium zonale*, and *Anadyomene stellata*; *Galaxaura obtusa* and *Kallymenia limminghei* were less common but

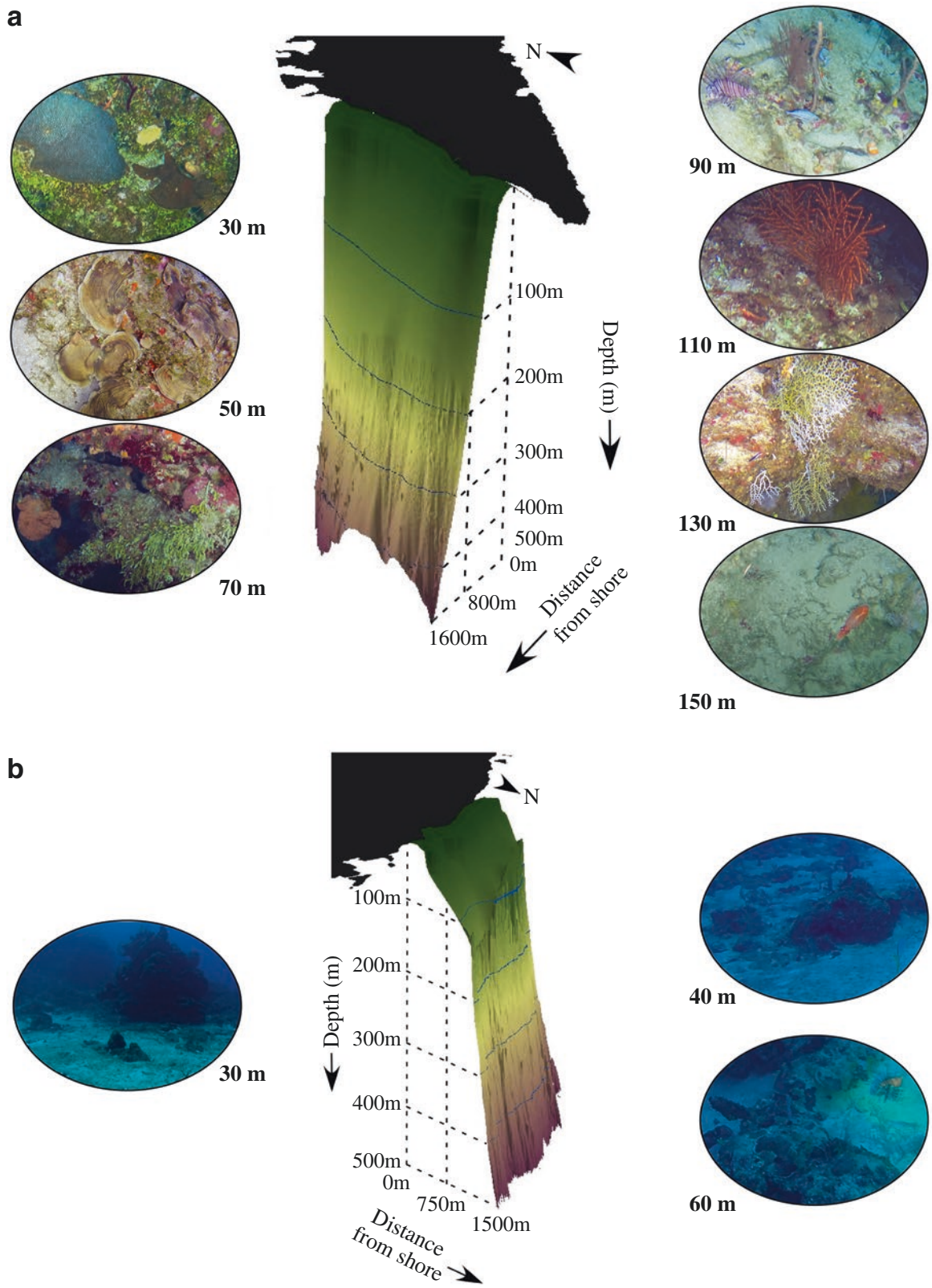

Fig. 5.4 (**a**) Multibeam three-dimensional depth profile from the southwest coast of Roatan, showing images of the reefs at 20 m intervals from 30 to 150 m depth. In this area MCEs are located on steep slopes (Photo credit: Erika Gress and Karl Stanley). (**b**) Multibeam three-dimensional depth profile from the northwest coast of Roatan. Images show MCEs at 30, 40, and 60 m depth. The extended platform at 40–60 m depth is mainly covered with sand and a few scattered small MCE patch reefs (Photo credit: Erika Gress). See Fig. 5.2 legend for locations and bathymetry sources

Table 5.1 Documented algae and scleractinian corals reported on MAR MCEs

Phylum	Family	Species	Reported observations		
			Mexico	Belize	Honduras
Cnidaria	Acroporidae	*Acropora cervicornis*[a]	X		
		A. palmata[a]	X		
	Agariciidae	*Agaricia* spp.	X	X	X
		A. agaricites		X	
		A. fragilis		X	
		A. grahamae		X	X
		A. lamarcki	X	X	
		A. tenuifolia	X		
		A. undata		X	X
		Helioseris cucullata	X	X	X
	Astrocoeniidae	*Madracis* sp.		X	
		Madracis auretenra	X		
		M. formosa			X
		M. pharensis			X
		M. senaria			X
		Stephanocoenia intersepta	X	X	X
	Meandrinidae	*Dichocoenia stokesii*		X	
		Eusmilia fastigiata	X		
		Meandrina meandrites	X	X	
	Merulinidae	*Orbicella* sp.[b]		X	
	Montastraeidae	*Montastraea cavernosa*	X	X	X
	Mussidae	*Colpophyllia natans*	X	X	
		Diploria spp.			X
		D. labyrinthiformis		X	
		Manicina areolata		X	
		Mycetophyllia aliciae	X	X	
		M. danaana		X	
		M. lamarckiana	X	X	
		M. reesi		X	
		Pseudodiploria strigosa	X	X	
		Scolymia cubensis		X	
		S. lacera		X	
		S. wellsii	X		
	Poritidae	*Porites* spp.			X
		P. astreoides	X	X	
		P. divaricata	X		
		P. furcata		X	
	Scleractinia incertae sedis	*Solenastrea* sp.		X	
	Siderastreidae	*Siderastrea siderea*	X	X	X
Chlorophyta	Anadyomenaceae	*Anadyomene gigantodictyon*	X		
		A. stellata		X	
	Boodleaceae	*Phyllodictyon anastomosans*	X		
	Codiaceae	*Codium taylorii*		X	
	Halimedaceae	*Halimeda* spp.	X	X	
		H. copiosa		X	
		H. discoidea		X	
		H. opuntia		X	
		H. simulans		X	
	Siphonocladaceae	*Dictyosphaeria cavernosa*		X	
		D. ocellata		X	
	Udoteaceae	*Penicillus capitatus*		X	
		P. dumetosus		X	
		Rhipocephalus phoenix		X	
		Udotea conglutinata		X	
		U. cyathiformis		X	
		U. flabellum		X	

(continued)

Table 5.1 (continued)

Phylum	Family	Species	Reported observations		
			Mexico	Belize	Honduras
Ochrophyta	Dictyotaceae	*Dictyota dichotoma*		X	
		Lobophora variegata		X	
		Stypopodium zonale		X	
	Sargassaceae	*Sargassum polyceratium*		X	
		Turbinaria tricostata		X	
Rhodophyta	Champiaceae	*Champia parvula*		X	
	Corallinaceae	*Amphiroa hancockii*		X	
		A. tribulus		X	
	Galaxauraceae	*Galaxaura obtusa*		X	
		G. rugosa		X	
	Kallymeniaceae	*Kallymenia limminghei*		X	
	Rhodomelaceae	*Laurencia intricata*		X	
	Rhodymeniaceae	*Botryocladia pyriformis*		X	
	Solieriaceae	*Wurdemannia miniata*		X	

[a]Observations only at 30–31 m in Chinchorro Atoll, Mexico, during 1983–1984 (Zlatarski 2007)
[b]Originally reported as *Montastraea annularis* (James and Ginsburg 1979; Cairns 1982; Rützler and Macintyre 1982), which has since been divided into three species and revised as genus *Orbicella*

only found at deeper depths (Norris and Bucher 1982). There have also been sightings of a large bloom of *Anadyomene gigantodictyon* near Carrie Bow Cay, covering on average 30% of the benthos at 51–60 m deep along approximately 0.5 km section of MCE known as South Reef (Littler and Littler 2012). It is important for future work to expand algal surveys to another MAR MCE locations.

5.4.2 Anthozoans

Scleractinians. Zooxanthellate hard corals have been documented down to 55 m in Mexico (Gress et al. 2018), although research on deeper MCEs has not been conducted. The deepest recorded colonies to date in Belize are *Montastraea cavernosa* at 95 m off Tobacco Cay and *Agaricia fragilis* at 102 m on the eastern margin of Glover's Reef (James and Ginsburg 1979). In Honduras, the maximum observed hard coral depths were 85 m in Utila (Laverick et al. 2017) and 91 m in Roatan (Gress, per. obs.). Similar to other geographical regions (Baker et al. 2016), hard corals take on a more plate-like morphology or are found as small individual colonies at increased depths (Graus and Macintyre 1976; Miller and Macintyre 1977; James and Ginsburg 1979).

Hard coral cover declines rapidly with depth along the slope on most studied MAR MCEs. For example, in Cozumel National Marine Park, hard coral cover was recorded as 9% at 15 m to 1% at 55 m (Gress et al. 2018). Around Utila, hard coral cover was 14% at 15 m but declined to 4% at 40 m (Andradi-Brown et al. 2016c). However, on steeper more exposed reef walls around Utila, hard coral cover has been recorded as 8%, 2%, and <1% at 55, 70, and 85 m, respectively (Laverick et al. 2017). Hard coral cover has not been quantified using transects on MCEs in Belize, though James and Ginsburg (1979) noted *Orbicella annularis* and *Agaricia* spp. between 37 and 45 m depth off Queen Cay grew in large overlapping plates, and constituted >25% of the benthic cover at all sites surveyed.

Around Cozumel, hard corals from the genera *Helioseris* and *Agaricia* were among the most common recorded at 55 m; however, colonies were small on average, with MCEs dominated by sponges, gorgonians, calcareous algae, and black coral communities (Günther 1990; Gress et al. 2018). This characteristic of few hard corals with foliose and encrusting formations at upper-mesophotic depths was reported in early qualitative observations from the 1980s on the west side of Cozumel (Jordán Dahlgren 1988; Zlatarski 2007). Other scleractinian species were documented in these early observations on Chinchorro Atoll and on the Mexican Caribbean mainland coast between 30 and 45 m depth (Table 5.1; Zlatarski 2007).

In Belize, James and Ginsburg (1979) observed hard coral species across the MCE depth gradient (Table 5.1). They reported *Orbicella* spp. and *Agaricia* spp. from 37 m down to the beginning of the wall at 65 m, followed by *A. grahamae*, *A. fragilis*, *M. cavernosa*, *Madracis* sp., *Solenastrea* sp., *Stephanocoenia* sp., and *Mycetophyllia reesi* at 70–80 m depth. On the upper margin of the mesophotic zone at 31 m, 42 species of hard corals have been verified from field samples (Cairns 1982). Cairns (1982) noted finding *Porites astreoides* to depths of >28 m, *M. cavernosa* to >26 m, *Dichocoenia stokesii* to 31 m, *Scolymia cubensis* from 30 to 40 m, as well as *Meandrina meandrites* and *Scolymia lacera* commonly on the fore-reef slope down to 40 m. Survey transects conducted from the seagrass flats eastward to the outer fore-reef slope just north of Carrie Bow Cay demonstrated relatively abundant plating colonies of *M. cavernosa*, *O. annularis*, *Helioseris cucullata*, and *A. fragilis* at 30 m (Rützler and

Macintyre 1982). While less abundant, *A. agaricites*, *A. lamarcki*, *P. porites*, *P. furcata*, *Diploria labyrinthiformis*, *Colpophyllia natans*, and *Mycetophyllia danaana* were all observed near 30 m in the vicinity of Carrie Bow Cay (Rützler and Macintyre 1982).

In Honduras, the most detailed mesophotic hard coral community composition analysis was conducted by Laverick et al. (2017) down to 85 m depth around Utila (Table 5.1). A total of 26 hard coral species were recorded on MCEs, with the majority of these species also found on shallow reefs. *A. grahamae*, *A. undata*, *M. formosa*, and *M. senaria* were only found below 25 m, while the only MCE coral species found exclusively deeper than 40 m was *M. pharensis.* In addition to those species, *H. cucullata*, *M. cavernosa*, *Siderastrea siderea*, and *S. intersepta* were also recorded reaching 70 m or deeper (Laverick et al. 2017). Also in Utila, there is evidence that historically extensive *Agaricia* spp. colonies were present at 70 m depth, although the majority of these colonies were dead when observations were conducted in 2015 (Laverick et al. 2017). In Roatan, benthic surveys were conducted by Mehrtens et al. (2001) down to 40 m, recording *Agaricia* spp., *Porites* spp., *Diploria* spp., and *Montastrea* sp. in the 30–40 m range.

Antipatharians. Black corals make up a major component of some MAR MCEs. In Cozumel, which has long been famed for its extensive MCE black coral populations, six black coral species have been recorded (Padilla Souza 2004). In Honduras, black corals have been observed on MCEs to >50 m depth around Barbareta Island (Fonseca et al. 2004), though their exact population density and composition has not been established. Around Cayos Cochinos, Honduras, five species of black coral have been recorded from surveys down to 35 m depth (Guzman 1998).

5.4.3 Sponges

Sponges have been poorly studied on most MCEs in the MAR. The few studies conducted suggest sponge cover on MCEs is highly variable. For example, in the Cozumel National Marine Park, sponge cover increased with depth from 25% at 15 m to 39% at 55 m (Gress et al. 2018). One study in Utila reported sponge cover declining with increased depth, from 4% at 15 m to 1% at 40 m (Andradi-Brown et al. 2016c), though another study recorded sponge cover of approximately 20% at several Utilian sites in the 40–70 m depth range (Laverick et al. 2017). Despite many publications on sponges from the Belize Barrier Reef, most sponge research has been limited to shallow reefs, which exhibit high sponge abundance and diversity (Rützler 2012). On the outer fore reef at Carrie Bow Cay, demosponges were recorded at about 10% cover, with 29 species found deeper than 30 m (Diaz and Rützler 2001). On the south of Carrie Bow Cay, the giant barrel sponge *Xestospongia muta* has been observed on the fore-reef slope to depths >60 m and was found to spawn deeper than 20 m (Ritson-Williams et al. 2005). Sponges make up a major component of benthic cover on some MAR MCEs, but further research is required to understand the complexity of observed patterns.

5.4.4 Fishes

Fish communities on MCEs in the MAR have been well documented, with several published studies. The earliest observations came from Belize below 50 m at Tobacco Reef, Queen Cays, and Glover's Reef (Colin 1974). On Utila, fish species richness, abundance, and biomass declined with increased depth across a 5–40 m depth gradient, though individual fish of several species were larger on deeper reefs when compared to shallower reefs (Andradi-Brown et al. 2016c). On the deeper portions of the Belize Barrier Reef, 33 fish species were recorded comprising 15 families (Colin 1974). At Glover's Reef transects were conducted at 90 m, where the commonest fishes observed were *Gramma melacara*, *Gramma* sp., *Lipogramma klayi*, *Liopropoma mowbrayi*, and *Serranus luciopercanus* (Colin 1974). More recent fish studies have focused on the reefs of Utila (Andradi-Brown et al. 2016b, c, d, 2017a, b, d). Common fishes observed on Utilian reefs in the 70–85 m depth range include the Sunshine fish (*Chromis insolata*) and blackfin snapper (*Lutjanus buccanella*) (Andradi-Brown et al. 2016b). Another deeper observation from Honduras includes the hourglass basslet (*Lipogramma levinsoni*) at 140 m off Roatan (Baldwin et al. 2016). The majority of fish species observed at 40 m around Utila are depth-generalist species, also found on adjacent shallow reefs (Andradi-Brown et al. 2016c). More detailed fish community surveys have been conducted to look at changes in reef fish biomass across a depth gradient. For example, several species of Scaridae were found at reduced proportions of community biomass on MCEs (Andradi-Brown et al. 2016c). Six species of fish, spanning several trophic groups, increased body size on MCEs compared to shallow reefs, *Acanthurus coeruleus*, *Chromis cyanea*, *Thalassoma bifasciatum*, *Clepticus parrae*, *Ocyurus chrysurus*, and *Scarus iserti* (Andradi-Brown et al. 2016c). Additionally, several locally threatened species, such as Caribbean reef sharks (*Carcharhinus perezii*), which are absent from shallow fringing reefs, were observed at depths >50 m (Andradi-Brown et al. 2016b). Other shark species, such as black nose shark (*Carcharhinus acronotus*), not previously reported in fisheries-independent monitoring data from Utilian fringing reefs have been observed at >40 m depth (Andradi-Brown et al. 2016d).

In Cozumel, Mexico, fish communities have been characterized by Gress et al. (2018). Of the total fish species identi-

fied, 9% were present only on MCEs, while 43% were recorded on both shallow and mesophotic reefs, including many commercially important fish species. This is similar to Honduras, where the majority of fish at 40 m were also present on shallow reefs (Andradi-Brown et al. 2016c). Of the major commercially important fishes in Cozumel, three families (Acanthuridae, Haemulidae, and Millidae) showed lower biomass at 55 m compared to 15 m, while one family showed greater biomass (Pomacanthidae) (Gress et al. 2018).

Non-native lionfish (*Pterois* spp.) have widely colonized shallow reefs and MCEs across the region (Andradi-Brown et al. 2017b, d). In 2010, lionfish were observed on Roatan MCEs at 122 m, making this one of the earliest MCE invasive lionfish records for Honduras (Schofield 2010). More recent observations from Roatan have extended into the upper-bathyal zone (200–1000 m depth), with lionfish observed down to 250 m (Gress et al. 2017). In Mexico, lionfish have been observed at 55 m (Gress et al. 2018) and in Belize at depths of 50 m (Voss and Eckert, pers. obs.), though it is likely that they extend deeper.

Across the MAR region, Muhling et al. (2013) studied the vertical depth distribution of fish larvae. While these samples were not directly taken on the reef, in many cases, they were taken in locations adjacent to reefs in Mexico and Belize. Muhling et al. (2013) reported larvae for common reef fish species such as *Thalassoma bifasciatum* were mostly restricted to shallow waters (< 50 m) during the day, with a few individuals in the 50–75 m range. At night individuals were collected down to the 75–100 m range. Many other common reef fish genera such as *Sparisoma*, *Scarus*, and *Acanthurus* larvae were identified as well but found to be limited to 40–60 m depth (Muhling et al. 2013). A reef-associated planktonic light-trapping study was conducted on shallow reefs (15 m) and MCEs (40 m) on Utila, finding no differences in fish larvae abundance between depths (Andradi-Brown et al. 2017c). However, these results are affected by limited sampling time, so do not account for known seasonality in fish larval recruitment (Luckhurst and Luckhurst 1977).

5.4.5 Other Biotic Components

Reef-associated MCE zooplankton studies have been conducted by Andradi-Brown et al. (2017c) in Honduras using light traps to collect plankton samples overnight. These samples suggested similar planktonic community richness and overall biomass across the depth gradient, but with high variation and differences between survey sites (Andradi-Brown et al. 2017c). Larger zooplankton organisms (>2 mm body size) were found to be more abundant on MCEs than adjacent shallow reefs. These larger organisms included groups such as decapod crab zoeae, mysid shrimps, peracarid crustaceans, and oligochaetes (Andradi-Brown et al. 2017c).

5.5 Ecology

The majority of detailed ecological work on MAR MCEs has been conducted on Utila and focused on hard coral or fish communities. Hard coral communities around Utila were studied by Laverick et al. (2017) across a 5–85 m depth gradient, with the aim of refining how to define a mesophotic coral community. To do this, multivariate statistical techniques were used to initially identify natural depth groupings of hard coral species based on different sites and depths and then to look at the depths of community transition between the groupings. Two groups of hard corals were found, a shallow specialist community and a depth-generalist community (Laverick et al. 2017). The shallow specialist community was dominant at 5 and 15 m, while the depth-generalist community was dominant at 40–85 m, although many coral species associated with the depth-generalist community were also present at 5 and 15 m, but at lower abundance, suggesting that other factors such as shallow-reef environmental conditions or competition with shallow specialist species could be limiting their abundance (Laverick et al. 2017).

Fish communities on MCEs contain a range of trophic groups, whose proportions depend on whether weighting by abundance or biomass. Planktivores, comprising 35% of the community, are the most numerous reef fishes at 40 m around Utila; though this is a lower proportion than the 63%, they comprise on adjacent shallow reefs (Andradi-Brown et al. 2016c). Piscivores are the largest trophic group by biomass at 40 m, making up 37% of the community, though herbivores and invertebrate feeders make up substantial community components (Andradi-Brown et al. 2016c). Herbivores are the largest group on shallow reefs; despite being present on MCEs, they decline as a proportion of the overall fish community with increased depth (Andradi-Brown et al. 2016c). On even deeper Utilian reefs in the 70–85 m range, herbivores are near-absent, and the most commonly observed fish species is the planktivorous sunshine fish (*Chromis insolata*) (Andradi-Brown et al. 2016b).

To better understand the relative roles of fishes in structuring benthic communities compared to other environmental variables, such as light, Andradi-Brown (2017) conducted a factorial experimental manipulation on reefs at 30–40 m depth on Utila. Results indicated that light plays a crucial role in structuring MCE benthic communities. While hard coral and sponge cover declined when fish were excluded, these results might have been caused by the reduction in water flow from the fish-exclusion cages. Therefore, despite the presence of herbivores on MCEs, they are unlikely to be the main structuring agents of Utilian MCE benthic macroalgal communities (Andradi-Brown 2017).

A wide range of fish survey techniques have been used to study MCE fish communities, both on the MAR, but also globally. Two studies have been conducted on the reefs of Utila to evaluate how the survey technique choice affects

biases in recorded MCE fish communities (Andradi-Brown et al. 2016d, 2017a). Diver-operated stereo-video (DOV) transects were compared with baited remote underwater video stations (BRUVS) on both shallow reefs and MCEs to identify depth-specific biases between these techniques (Andradi-Brown et al. 2016d). BRUVS consistently recorded more species than DOV on both shallow reefs and MCEs. Some of the identified differences between both techniques were found to vary with depth, with BRUVS better able to detect smaller fish on MCEs. Broadly, BRUVS were found to be better for recording all components of fish communities but took substantially longer to analyze. As well as being much quicker to analyze, DOV was reliable for surveying key functional groups such as herbivores. A second study on Utilian reefs evaluating how method choice affects recorded fish communities compared DOV transects filmed with open-circuit SCUBA on shallow reefs and MCEs with those filmed using closed-circuit rebreather (CCR) (Andradi-Brown et al. 2017a). The minimum approach distance (MAD), the distance at which divers could approach a fish before it moved away, was measured for both dive gear types. While CCR had lower MADs, implying divers could get closer to fishes using CCR than open-circuit SCUBA, the differences were not large enough to alter the detectability of most MAR fish families surveyed. However, for many fish families, regardless of dive gear choice, divers were able to approach individuals more closely on MCEs than shallow reefs, and larger fishes were warier of divers than smaller fish.

5.6 Threats and Conservation Issues

Many potential MCE threats, such as fishing pressure, harvesting of key benthic species, invasive species, sedimentation, and water pollution, have been identified (Andradi-Brown et al. 2016a; Gress et al. 2017, 2018). However, there is little long-term monitoring of MCE health in the MAR, and MCEs are rarely incorporated into marine-protected areas (MPAs). In 2016, an expanded MPA encompassing the majority of the Mexican Caribbean was announced. It comprises approximately 57,000 km^2 of marine habitats in the northern MAR area, with about 19,000 km^2 in core zones, and the rest in buffer zones. Legislation and management plans for this vast new area are still to be announced (Diario Oficial de la Federación 2016). Since 1982, an MPA network has been established in Belize, encompassing over 3600 km^2, approximately 20% of the country's territorial sea. No-take zones comprise roughly 14% of Belize's total established MPA area. In Guatemala, only about 62 km^2 of coral reef area is known, but over 900 km^2 of MPAs have been created mostly in Punta de Manabique reserve (Wilkinson 2008; Kramer et al. 2015). In Honduras, the entirety of the Bay Islands waters were designated a National Park in 1997 (Kramer et al. 2015). This protected area extends 12 nautical miles around the coasts of the Islands of Guanaja, Roatan, and Utila.

Management and enforcement of fisheries regulations on the southern MAR is generally weak, with overexploitation in many areas of Honduras (Gobert et al. 2005; Korda et al. 2008). Gobert et al. (2005) compared the relative contribution of the shallow-water and mesophotic fishery for snapper and grouper species throughout the Bay Islands of Honduras, finding that the mesophotic snapper fishery was significant in the region. Large (>500 mm) predatory fishes are rare on MCEs in both Cozumel and Utila, suggesting that these fisheries are having an impact on fish-length distributions (Andradi-Brown et al. 2016c; Gress et al. 2018). In Cozumel, there was little difference in MCE fish-length distributions when comparisons were made between locations inside the National Marine Park and locations without protection (Gress et al. 2018). This could suggest that depth is naturally acting as a refuge from fisheries, unfortunately, the lack of large predatory fish at both locations is likely an indicator that the existing shallow-focused marine park is not providing protection for mesophotic fish communities (Gress et al. 2018). There is some evidence of MCEs acting as fish refuges on the MAR. The north coast of Honduras historically had a large shark fishery leading to shark population declines (Box and Canty 2011). This fishery was restricted in 2010 (Box and Canty 2011), though many shark species that were historically present on Utilian shallow reefs remain absent. Recently, some of these shark species have been recorded on MCEs (Andradi-Brown et al. 2016b, d), suggesting that MCEs may offer protection for some sharks.

During 2015, Laverick et al. (2017) observed extensive dead plating *Agaricia* spp. at 70 m depth in Utila, suggesting there were large colonies at these depths. Andradi-Brown (2017) monitored reef areas at 30–40 m depth at one site on Utila, using permanent photo-quadrats over an 18-month period during 2015–2016. While their study was not intending to monitor background changes in reef health, they detected a slight, but significant, decline in hard coral cover over this short period (Andradi-Brown 2017). During a coral bleaching event in 2015, Laverick and Rogers (2018) conducted a transplant experiment on Utila, moving fragments of *A. lamarcki* between shallow and mesophotic depths along with controls. They found that fragments placed at mesophotic depths had lower bleaching rates and greater survival than fragments placed on shallow reefs. However, bleaching was observed in MCE fragments and in *A. lamarcki* colonies around Utila down to 35 m depth (Laverick and Rogers 2018).

Sedimentation is a major threat to reefs in the MAR region and has long been highlighted as a key issue to address (Harborne et al. 2001). In Banco Capiro, an offshore reef in Tela Bay, on the Honduran mainland, some preliminary dives looking for MCE communities were conducted to 42 m during 2015. Despite having the highest shallow-reef coral

cover reported in the MAR (Bodmer et al. 2015), no MCEs were observed. Instead, at the base of the offshore bank, an extensive sediment bed was found smothering patch reefs comprised of dead coral skeletons that still had some fishes associated with them (Andradi-Brown, pers. obs.).

Cozumel has long been famed for its extensive mesophotic black coral populations and the associated black coral jewelry industry (Kenyon 1984). The majority of the jewelry is made from *Antipathes caribbeana* and *Plumapathes pennacea*, as these species form the largest colonies, with skeletons that are cut, polished, and then handcrafted into jewelry. In the Mexican Caribbean, the earliest records of black corals harvesting date from the early 1960s. While the availability of black coral jewelry on Cozumel has declined in recent years, shops selling black coral jewelry and handcrafts are still widespread (Gress, pers. obs.). Regional harvest rates reported from the 1980s to early 1990s were between 1000 and 1500 kg of gross product per year, causing overexploitation of black coral in the area (Padilla and Lara 2003). Declining black coral population densities in Cozumel have been observed since the 1970s fishers, although no population assessments were conducted until the late 1990s. In 1994, three species of black corals were included in the Mexican Official Norm that lists national threatened species under special protection: *Antipathes dichotoma* (wrongly cited as *A. bichitoena*), *A. grandis*, and *A. ulex* (wrongly cited as *A. ules*) (Padilla and Lara 2003). The inclusion of these three species was however a mistake, as they have not been recorded in Mexican waters on either the Atlantic or Pacific coast (Opresko and Sanchez 2005). The absence of these species was revealed by the first population assessment conducted in 1998 (Padilla Souza 2004). The only other population assessment, allowing changes in population density and colony size for the two primary harvested species to be calculated, was conducted during summer 2016 (Gress and Andradi-Brown 2018). Results indicate that the *P. pennacea* population density has severely declined, though the remaining mesophotic colonies are larger on average than those recorded in the 1990s, suggesting that there is low recruitment or juvenile survival rates (Gress and Andradi-Brown 2018).

Non-native lionfish are highly abundant on MCEs in some locations in the MAR, such as the Bay Islands of Honduras (Gress et al. 2017; Andradi-Brown et al. 2017b, d) but at lower densities on MCEs in other areas such as Cozumel (Gress et al. 2018). The greatest density recorded on MAR MCEs is in Utila, where lionfish reached 3.0 individuals per 250 m^2 at 70 m and were found to be feeding on native fishes (Andradi-Brown et al. 2017b). While lionfish are known to exhibit ontogenetic migrations across shallow tropical marine habitats (Claydon et al. 2012), it is not clear whether these extend to MCEs. Utilian MCE lionfish behaviorally respond to divers in similar ways as lionfish populations previously exposed to culling in shallower reefs (i.e., skittish) (Andradi-Brown et al. 2017b), supporting the idea of ontogenetic migration. Yet, culling alters lionfish body-size distributions (Frazer et al. 2012), making ontogenetic migrations difficult to detect in areas with depth-restricted culling. See Andradi-Brown (2019) for a review of lionfish on MCEs. Work on Utila has identified that lionfish on MCEs are larger, and females are more mature for their body size than individuals found in adjacent shallow reefs (Andradi-Brown et al. 2017b, d). Concern has been raised whether substantial mesophotic populations could be undermining current lionfish management, which is broadly shallow-reef focused (Andradi-Brown et al. 2017d). Taken together, these observations suggest that MCE health on the southern MAR is likely declining, though more research and long-term monitoring is required to establish this across the region.

5.7 Conclusion

MCE research in the MAR is still in an early stage, with the majority of studies conducted restricted to a few key sites such as Cozumel, the atolls of Belize, Utila, and to a lesser extent Roatan. We were unable to identify any MCE studies from Guatemala. In addition, much of the MCE research conducted in the region has focused on upper MCEs, with few quantitative surveys conducted on lower MCEs (60–150 m). Existing studies are also site-specific, with no directly reef-associated studies incorporating multiple geographical locations along the length of the MAR to test for regional patterns. These are major knowledge gaps that future studies should address. Many threats to MCEs on the MAR are common throughout the Caribbean and wider western Atlantic, and there is an urgent need to address these. As the second largest reef system in the world, with four countries involved in management, this will inevitably be complex. However, because of their inherent biodiversity, and the potential role that MCEs may play underpinning overall reef resilience, it is crucial to better incorporate them into reef management plans.

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