

Puerto Rico

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Abstract

Mesophotic coral ecosystems (MCEs) in Puerto Rico cover a potential area of 2180 km² or 38% of the total area from the shoreline to 150 m. MCEs occur primarily along the upper insular slope of the Puerto Rico-Virgin Islands platform. Patchy MCE development occurs along the insular slope, with distribution strongly related to geomorphology. Shallow mesophotic platforms can support well-developed coral communities dominated by the *Orbicella annularis* species complex, but deep mesophotic platforms are more poorly developed and consist primarily of algae and sponges, with patchy occurrences of corals, dominated by *Agaricia* spp. Macroalgae, with 185 taxa, are the dominant component of MCEs, both in species richness and percent cover. The dominant algal components below 40 m are calcified encrusting red algae including Corallinales and Peyssonneliales species.

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Twenty-seven scleractinian corals and two hydrocorals were recorded within MCEs. Dominant corals in shallow MCEs were *Orbicella* spp., *Siderastrea siderea*, and *Porites astreoides*, but by 50 m *Agaricia* dominates, particularly *A. undata*, *A. lamarcki*, and *A. grahamae*. Over 100 fish species have been recorded from mesophotic depths, with *Chromis insolata* being the most common and abundant species. High vertical connectivity appears to occur within fishes, with a significant component potentially dependent on shallow, nearshore nursery areas. For all taxa, species richness and abundance decreased with depth, and changes in community structure were observed, with noted breaks occurring at ~45 and ~60 m. Primary local threats to Puerto Rico's MCEs are overfishing, invasive species, and land-based anthropogenic inputs that increase turbidity and sedimentation.

Keywords

Puerto Rico · Mesophotic coral ecosystems · Geomorphology · Species distributions · Threats

7.1 Introduction

Puerto Rico, located in the northeast Caribbean, is the smallest and easternmost island of the Greater Antilles. It shares the Puerto Rico-Virgin Islands (PR-VI) platform with the US and British Virgin Islands to the east. To the west is the Mona Channel, where depths range from 300 to 1000 m. Within the Mona Channel lie the islands of Mona and Monito (45 km west of the Puerto Rico insular platform), Desecheo Island (21 km off the west coast), and submerged banks including Pichincho and Bajo de Sico, rising to depths of 50 and 25 m, respectively (Fig. 7.1). Defining the mesophotic depth range as 30–150 m, the total area of potential mesophotic coral ecosystem (MCE) development in Puerto Rico is 2180 km², which constitutes 38% of the total area from the shoreline to

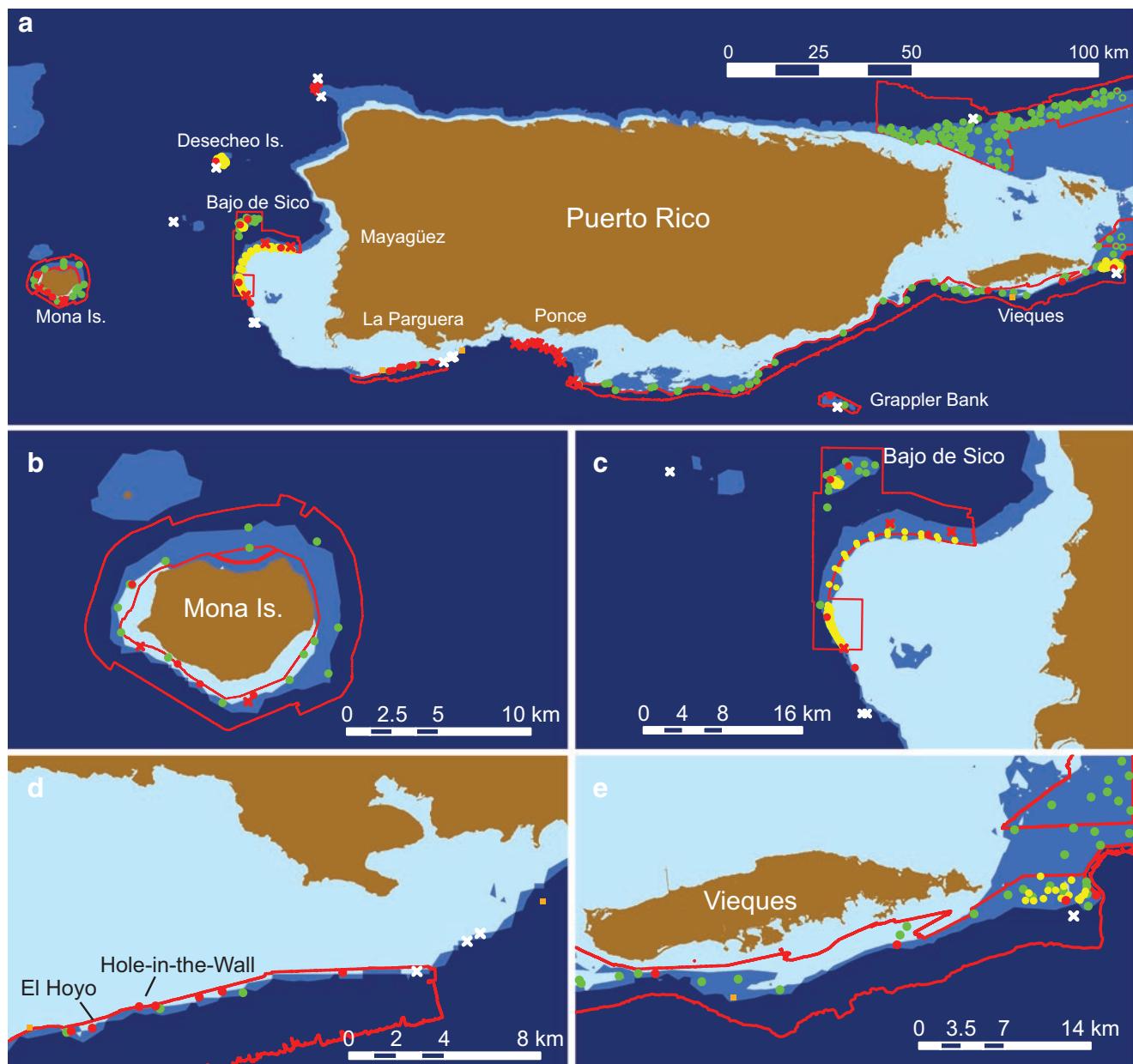


Fig. 7.1 MCE sampling locations in (a) Puerto Rico, (b) Mona Island, (c) the northwest platform and Bajo de Sico, (d) La Parguera, and (e) Vieques. White "X" = Johnson Sea Link submersible dive sites. Orange squares = AUV dives. Green circles = NOAA/National Centers for Coastal Ocean Science drop camera/ROV sites. Yellow circles = shallow (<50 m) dive sites by García-Sais et al. (2004, 2010, 2011, 2012). Red circles = combined deep-dive (photo-transect surveys) and ROV sites by the authors, with red "X" = additional ROV sites. Areas outlined in red indicate areas with high-resolution multibeam bathymetry

150 m. The purpose of this chapter is to review existing literature and present new information to characterize the MCEs of Puerto Rico in terms of their geomorphology, physical environment, and biodiversity and to integrate these to describe their ecology, emphasizing the factors and processes that influence community composition.

7.1.1 Research History

Until recently, knowledge of MCEs in Puerto Rico was limited to exploratory surveys using fish traps, dredges, and conventional SCUBA diving. Most of the latter, in particular, was centered off La Parguera on the southwest coast where the

Magueyes Island Marine Laboratory of the University of Puerto Rico's Department of Marine Sciences (UPR-DMS) is located. This work led to the discovery and description of new species and range extensions (e.g., Starck and Colin 1978; Dennis et al. 2004; Van Tassell et al. 2012; Ballantine et al. 2016), as well as documented the vertical extent of scleractinian corals (e.g., Acevedo et al. 1989). In 1985, a series of submersible dives using the *Johnson Sea Link* were conducted around Puerto Rico (Nelson and Appeldoorn 1985), with many of these including habitats shallower than 150 m (Fig. 7.1). Among these were two dives dedicated to mesophotic depths looking at fishes and benthos off La Parguera. These dives provided the most comprehensive descriptions of the deep reef in Puerto Rico until the twenty-first century.

The pace of mesophotic studies increased dramatically after 2000 due to the advent and availability of new technology. This research was led by four research programs, three originating within the UPR-DMS. The first used the SeaBED autonomous underwater vehicle (AUV) at three sites to conduct photo-transects down the insular slope (Armstrong et al. 2002, 2009; Rivero-Calle et al. 2009) to characterize benthic cover (Fig. 7.1). The second used rebreather diving to conduct visual transects and characterize the benthic and fish communities with MCEs down to 50 m at six sites along the south and west coasts and in the Mona Channel (Fig. 7.1; García-Sais 2010; García-Sais et al. 2010, 2011, 2012). The third study used mixed-gas rebreather diving and a remotely operated vehicle (ROV) to characterize MCEs from 50 to 100 m, with a focus at 50 and 70 m, where high-resolution photo-transects and fish visual surveys were conducted. Initial work occurred at multiple sites off La Parguera (Fig. 7.1), with community structure related to depth, physical oceanography, geomorphology, and sediment dynamics (e.g., Sherman et al. 2010, 2016; Bejarano et al. 2014). Additional surveys were made off Ponce on the south coast to characterize an area heavily impacted by sedimentation (Appeldoorn et al. 2016a). This same team then conducted a series of three cruises, applying the same methodology at sites within the Mona Channel and along the west and south coasts of Puerto Rico (Fig. 7.1; Sherman et al. 2013). The fourth program consisted of a series of cruises wherein MCEs were mapped with multibeam bathymetry (NCCOS 2004–2006) and characterized using ROVs or drop cameras. This work primarily focused on several marine protected areas located around Puerto Rico and in the Mona Channel (Fig. 7.1). The third and fourth programs were both supported by the National Oceanic and Atmospheric Administration's National Centers for Coastal Ocean Science, with the third program as part of the Deep Coral Reef Ecosystem Studies Program (Deep CRES) designed to improve the understanding of MCEs and their relationship to shallower reefs.

7.2 Environmental Setting

Puerto Rico is situated in the northeast Caribbean Sea, effectively bordering the Atlantic Ocean. The north, east, and west coasts experience semidiurnal Atlantic tides and the south coast, diurnal Caribbean tides. Proximity to the Caribbean M2 and S2 amphidromic points (semidiurnal lunar and solar tides) ensures relatively small (≤ 0.5 m) tidal ranges. Mona Island, located west of Puerto Rico in the Mona Channel, experiences mixed-diurnal tides of similar range. Currents, especially on the relatively protected south coast, were long thought to be dominated by the near-constant easterly trade winds (see Bush et al. 1995 and references therein). Recent extended acoustic Doppler current profiler (ADCP) deployments off Puerto Rico's southwest coast (Schmidt 2010) indicate that despite the micro-tidal environment, currents below about 5 m are dominated by tidal influences and exhibit a distinct net offshore (south-southwest) component, a plausible response to a northward Ekman transport. This was demonstrated using ADCP/temperature instruments placed at 20, 40, 60, and 80 m depth off Puerto Rico's south coast (~8 km south of La Parguera; Schmidt, unpubl. data). The east-west component from the 20 m instrument (Fig. 7.2, top) reflected tidal reversals of the coastal currents. The composite record of the instruments at 40, 60, and 80 m (Fig. 7.2, bottom) also indicated that the tidal signal extends to at least 80 m, albeit attenuated. Near-surface flows are dominated by trade wind stress, with intermittent reversals due to brief wind shifts. Between about 5 and 30 m depths, currents typically reach 0.3–0.4 m s $^{-1}$. Below this depth, currents decrease to about 0.1 m s $^{-1}$ near bottom at 80 m (Schmidt unpubl. data).

Sediment transport studies (Sherman et al. 2016) suggest that even modest trade wind-driven surface waves can have effects on sedimentation to at least 70 m, perhaps by initiating downslope movement of shallower sediments. Also noted along the south coast, internal waves propagating along the seasonally varying thermocline (~20 to 80 m) regularly impact the steep insular slope, and mesoscale eddy impingements are also frequent (Schmidt unpubl. data). Effects of the latter remain poorly described but are thought to also modulate coastal currents.

The water column below 40 m appears to be weakly stratified, with the thermocline starting between 40 and 60 m and extending to below 80 m. At 40 m, temperatures mostly track seasonal surface temperatures (26–29.8 °C). Exceptions occur during the passage of particularly large amplitude internal waves. At 80 m, temperatures are mostly below the thermocline, but during fall and winter, internal wave troughs, and the thermocline, can reach as deep as 80 m. In contrast, sites at 60 m depth are routinely subjected to large

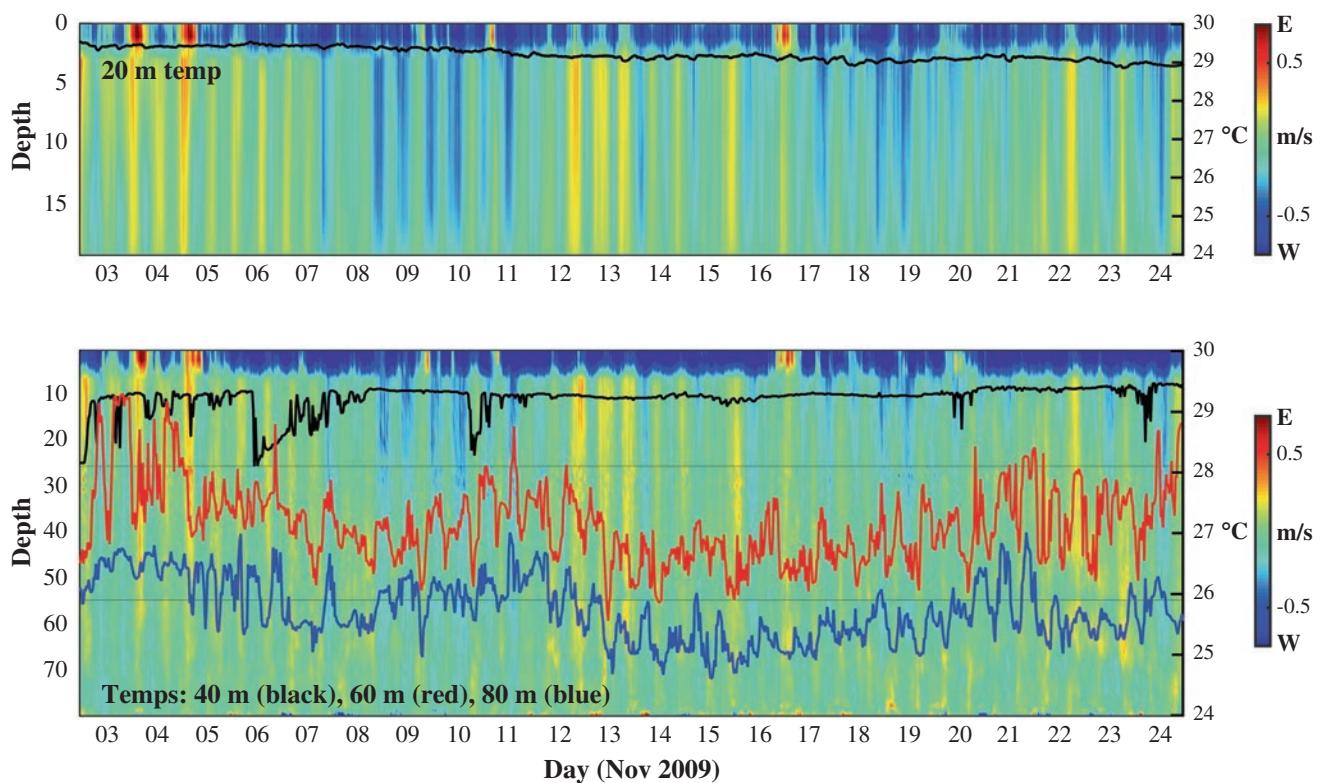


Fig. 7.2 Composite east-west (along shore) current profiles with depth from an array of ADCPs off La Parguera, Puerto Rico. Top, surface profile on the platform, with temperature record from 20 m. Bottom, profile along the insular slope, with temperature records from 40, 60, and 80 m. (Schmidt, unpubl. data)

amplitude internal waves, which may result in rapid temperature changes of up to 3 °C (Appeldoorn et al. 2016b).

7.3 Habitat Description

MCEs in Puerto Rico occur primarily along the upper insular slope of the PR-VI platform. The development of MCEs is strongly associated with slope geomorphology, which can be roughly divided into four classes based on slope gradient (Fig. 7.3). Little MCE development occurs along vertical walls. Shallow mesophotic platforms (<40–50 m) can support well-developed coral communities dominated by the *Orbicella annularis* species complex, as observed off Vieques at Black Jack Reef and El Seco (García-Sais et al. 2004, 2011). Deep mesophotic platforms (>40–50 m), as observed on offshore areas such as the north slope of Bajo de Sico and the top of Grappler Bank, are more poorly developed and consist primarily of algae and sponges, with patchy occurrences of corals, dominated by *Agaricia* spp. (Sherman and Appeldoorn 2015).

Off southwest Puerto Rico, the insular shelf extends 8–9 km offshore where a band of submerged reefs form a variable and discontinuous elevated rim along the shelf-edge

at depths of 15–25 m (Hubbard et al. 1997; Ballantine et al. 2008). The seaward fronts of these reefs extend to mesophotic depths. From the shelf break at depths of ~20 m down to depths of ~90 m, slope gradients range from ~25 to 45°. At depths of ~90 m, a steep, near-vertical wall begins that extends to depths of ~160 m (Sherman et al. 2010). The top of this feature typically marks the local depth limit of zoxanthellate scleractinian coral growth.

A systematic relationship exists between orientation of the insular shelf margin and geomorphology of the upper insular slope (Sherman et al. 2010). Southeast-facing slopes, more exposed to prevailing seas, tend to have a gentler gradient of ~29° and low rugosity/relief. In contrast, more sheltered southwest-facing slopes are steeper, with gradients of ~44° and an irregular topography consisting of steep-sided buttresses separated by narrow sand chutes (Sherman et al. 2010, 2016). MCEs are best developed on these steeper, sheltered slopes. Even within an area, changes in slope can have a profound impact on MCE development. For example, on the slope off Vieques Island, the bottom between 40 and 60 m was sparsely colonized hard ground, but below this there was a marked increase in gradient down to 70 m. Between 60 and 70 m, there was an abundant cover of plate-like corals (e.g., *Agaricia* spp.), *Madracis* sp., and other

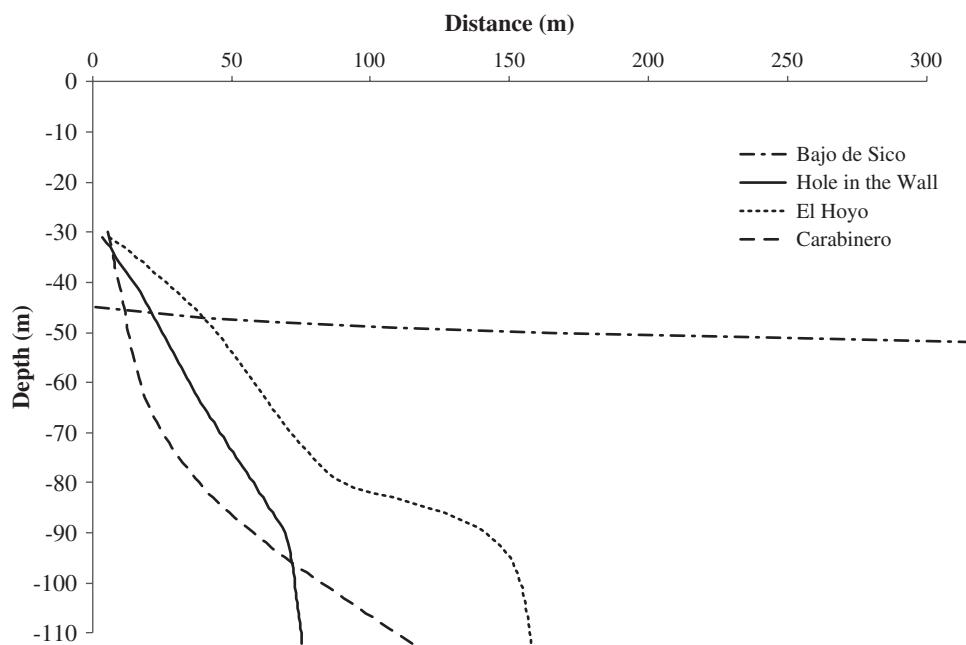


Fig. 7.3 Examples of slope inclinations at mesophotic depths from Puerto Rico: wall (Carabinero, Mona Island), steep slope (HW, La Parguera), gradual slope (EH, La Parguera), and platform (Bajo de Sico). See Fig. 7.1 for site locations (Nemeth and Appeldoorn, unpubl. data)

corals, along with macroalgae and sponges. Below 70 m the gradient again decreased and transitioned to a sandy slope at the bottom. High-resolution bathymetry showed this steep feature to extend for over 5 km, making this a potentially key area of MCE development (Appeldoorn, pers. obs.).

On steep insular slopes, MCEs are subject to persistent downslope transport of sediment generated by the production and breakdown of carbonate material at shallower shelf-edge reefs. Downslope bed-load transport is a chronic process much greater in volume than the vertical flux of sediments to the seafloor in these settings, though it is highly variable both spatially and temporally (Sherman et al. 2016). On low-gradient slopes, downslope transport tends to be spread over a broader area potentially inhibiting coral recruitment and growth. On steep, irregular slopes, transport is effectively funneled into narrow chutes, facilitating coral growth on intervening buttresses (Sherman et al. 2016). Thus, the interplay of slope geomorphology and sediment dynamics can exert an important influence on the occurrence and distribution of insular-slope MCEs.

(Ballantine and Aponte 2002; Ballantine et al. 2015). Three depth distributional groups may be thought of as comprising the mesophotic flora: shallow to mesophotic depths, intermediate to mesophotic depths, and restricted to depths >35 m. Nearly half of the species (81 spp.) in depths of 35 m or greater are found across the entire shelf (in southwest Puerto Rico), ranging from shallow, nearshore habitats to the offshore mesophotic. There is a tendency for many of these species to drop out of the flora toward the deeper mesophotic. Only approximately a quarter of these broadly depth-tolerant species are found in water deeper than ~60 m. Thus, community composition gradually changes with depth, both by the elimination of shallow species and the inclusion of mesophotic-restricted species. A second distributional group consists of macroalgae (~42 spp.) that are found ranging from intermediate depths (10–20 m) to the mesophotic realm. More than half of these are also found at depths greater than ~60 m. The third, slightly smaller, group of macroalgae (with few minor exceptions), made up by 38 species (and accounting for 8% of the total Puerto Rican macroalgal flora), appear to be depth restricted to water greater than 35 m in depth.

Replicate photo-transect surveys at 46, 59, and 70 m were conducted off La Parguera at El Hoyo (EH) and Hole-in-the-Wall (HW) and analyzed for percent benthic cover (Table 7.1). At these depths, macroalgae were the dominant benthic taxon. While substantial variation is seen in these data with respect to algal cover, undoubtedly a reflection of its patchiness, algal cover was in all cases greater than either coral or sponge, with sponge cover always greater than coral

7.4 Biodiversity

7.4.1 Macroalgae

Ballantine et al. (2016) reported 185 taxa of macroalgae comprising the deepwater, mesophotic flora of Puerto Rico. The species occurring at depths greater than 30 m represented a third of the total macroalgal flora known from Puerto Rico

Table 7.1 Percent cover of algae, sponge, and corals recorded in photo-transect surveys at three depths (46, 59, and 70 m) each at two sites (EH and HW) off La Parguera, Puerto Rico (Ruiz unpubl. data)

Benthic taxon	Percent cover						
	El Hoyo			Hole-in-the-Wall			Average
Depth (m)	46	59	70	47	57	76	
Rhodophyta (calcified, crustose)							
<i>Peyssonnelia flavescens</i>	1.8	0.0	0.0	4.6	5.8	0.0	
<i>Peyssonnelia iridescent</i>	0.0	0.3	0.0	0.0	0.0	0.0	
<i>Peyssonnelia gigaspora</i>	0.0	1.3	0.0	0.0	1.3	5.9	
<i>Peyssonnelia</i> sp.1	0.0	3.8	1.8	2.7	0.0	0.0	
<i>Peyssonnelia</i> sp.2	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Wrangelia</i> spp.	0.0	0.5	0.0	47.6	14.8	0.0	
<i>Hydrolithon abyssophila</i>	6.4	14.0	28.9	2.1	10.9	21.0	
Total Crustose Calcified	8.2	19.9	30.7	57.0	32.8	26.9	29.3
Heterokontophyta							
<i>Dictyota</i> spp.	6.0	14.7	0.0	2.1	14.3	0.0	
<i>Lobophora variegata</i>	30.5	5.8	0.5	13.5	11.8	1.7	
Chlorophyta							
<i>Microdictyon boergesenii</i>	0.0	5.3	0.0	0.0	1.2	0.0	
<i>Halimeda copiosa</i>	0.0	0.0	13.7	0.0	0.0	0.0	
<i>Halimeda goreaui</i>	0.0	2.1	0.0	0.6	0.0	0.0	
Cyanophyta							
<i>Schizothrix</i> sp.	21.6	0.6	0.0	0.0	0.0	0.0	
Turf	5.2	10.1	11.6	0.0	3.9	0.0	
Total algal cover	71.5	58.5	56.5	73.2	64.0	28.6	58.7
Coral	0.8	1.9	11.6	8.8	14.0	47.6	14.1
Sponge	14.4	16.3	16.0	12.6	11.4	5.4	12.7
Total living cover	86.7	76.7	84.1	94.6	89.4	81.6	85.5
% algal cover of living cover	82.5	76.3	67.2	77.4	71.6	35.0	68.7
% crustose calcified algal cover of living benthos	9.5	25.9	36.5	60.3	36.7	33.0	34.2

cover. In total, algal cover averaged 51.8%, sponge 16.5%, and coral 12.2%. Among the principal macroalgal species, the phaeophycean *Lobophora* spp. cover ranged from 0.5% to 30.5% (average = 10.3%) with no consistent pattern based on depth discernible from the limited dataset (Ballantine and Ruiz unpubl. data). There are now known to be at least three *Lobophora* species in Puerto Rico that have historically been referred to *L. variegata*. *Dictyota* species were also variably present (0–14.7%) and generally most abundant at the 59 m depth. Chlorophyta species, particularly *Halimeda* spp., were commonly observed but only abundant at 70 m (e.g., *Halimeda copiosa* at EH). The dominant benthic life forms at these depths at all sites were calcified encrusting red algae including Corallinales species and a number of recently described (Ballantine and Ruiz 2010) and undescribed peyssonneliaceous species. These crustose algal species comprised from 8.2% to 30.7% of all benthic biota, averaging over a third of the living benthic flora. One of the most abundant of the encrusting deepwater algal species at all sites in southwest Puerto Rico (>60 m) is *Hydrolithon abyssophila*. At these depths its cover ranged from ~10% to nearly 30%. This red crustose coralline alga may be the most abundant species based on cover below 60 m in deepwater habitats

around Puerto Rico and likely is the dominant organism throughout the Caribbean basin (Ballantine et al. 2016).

Within the mesophotic, algal species composition was seen to change with depth between approximately 30 and 70 m. There was a fairly high similarity in species composition between 30 and 50 m (68%). The species similarity between 30 and 70 m falls to 54%, or roughly half of the species are cosmopolitan across these depths. There was also a fairly high similarity between 50 and 70 m (67%). This would suggest an approximate depth of rapid change at about 50 m.

7.4.2 Anthozoa

Recent studies off La Parguera provide the most comprehensive description of mesophotic coral communities in Puerto Rico. Overall, 24 zooxanthellate and 3 azooxanthellate scleractinian species and 2 hydrocorals (*Millepora alcicornis* and *Stylaster roseus*) were identified at mesophotic depths down to 90 m (Table 7.2; Fig. 7.4). All but seven (28%) species (*Agaricia undata*, *A. grahamae*, *A. fragilis*, *Leptoseris cailleti*, *Madracis formosa*, *M. pharensis luciphila*, and *Mycetophyllum ressi*) are common in shallow water (Table 7.2). *M. pharensis*

Table 7.2 Depth distribution ranges of scleractinian and hydrocoral (*Millepora* and *Stylaster*) species observed in the field and/or identified from videos or high-resolution photographs off southwest Puerto Rico from 40 to 90 m in depth

Species	Depth range (m)					
	0–10	10–20	20–40	40–60	60–80	>80
<i>Agaricia fragilis</i>			x	x	x	
<i>Agaricia grahamae</i>			x	x	x	x
<i>Agaricia lamarcki</i>	x	x	x	x	x	x
<i>Agaricia undata</i>				x	x	x
<i>Astrangia solitaria</i> ^a		x	x	x		
<i>Dichocoenia stokesi</i>	x	x	x			
<i>Eusmilia fastigiata</i>	x	x	x	x		
<i>Helioceris cucullata</i>	x	x	x			
<i>Leptoseris cailleti</i>				x	x	x
<i>Madracis auretenra</i>	x	x	x	x	x	
<i>Madracis decactis</i>	x	x	x	x		
<i>Madracis formosa</i>			x	x	x	
<i>Madracis pharensis pharensis</i> ^a		x	x	x	x	x
<i>Madracis pharensis luciphila</i>			x	x	x	
<i>Montastraea cavernosa</i>	x	x	x	x	x	x
<i>Mycetophyllum aliciae</i>		x	x	x		
<i>Mycetophyllum reessi</i>			x	x		
<i>Orbicella faveolata</i>	x	x	x	x		
<i>Orbicella franksi</i>	x	x	x	x		
<i>Porites astreoides</i>	x	x	x	x	x	
<i>Rhyzosmilia maculata</i> ^a			x	x	x	
<i>Siderastrea siderea</i>	x	x	x	x		
<i>Stephanocoenia intersepta</i>	x	x	x	x	x	
<i>Scolymia cubensis</i>		x	x	x	x	
<i>Meandrina meandrites</i>	x	x	x			
<i>Undaria agaricites</i>	x	x	x	x	x	x
<i>Undaria humilis</i>	x	x	x	x	x	
<i>Millepora alcicornis</i>	x	x	x	x		
<i>Stylaster roseus</i>	x	x	x	x		
Total scleractinian	15	19	25	24	16	7
Total hydrozoans	2	2	2	2		
% shallow-water spp.	100	100	85	70.9	62.5	57
% mesophotic spp.			15	29.1	37.5	43

Species in bold are considered mesophotic species

^aAzooxanthellate species

luciphila was observed at 70 m, but *M. formosa* was not observed below 50 m. *Agaricia undata*, *A. grahamae*, and *Mycetophyllum reessi* are common deep mesophotic species throughout the Caribbean, although they constitute new reports for Puerto Rico. *Leptoseris cailleti* was previously reported only at Bajo de Sico, off the western platform of Puerto Rico (Dinesen 1980). Additionally, the local and geographic depth range of several shallow-water species has been expanded. For example, *Mycetophyllum aliciae* and *Madracis auretenra* (= *M. mirabilis*) occur down to 50 m; *Stephanocoenia intersepta*, *Madracis decactis*, *M. pharensis*, *Undaria agaricites*, and *Porites astreoides* down to 70 m; and *A. lamarcki* and *Montastraea cavernosa* down to 90 m (Table 7.2).

There is high variability in the composition, abundances, and live cover of scleractinians and other major benthic groups across depths within localities and between localities.

Upper mesophotic habitats (≤ 40 m) were dominated by shallow-water species *Orbicella* spp., *Siderastrea siderea*, *Porites astreoides*, *S. intersepta*, *Madracis* spp., and *Undaria* spp., similar to that observed further east along the southern PR-VI platform (Armstrong et al. 2006; Armstrong 2007; Smith et al. 2010). The genus *Agaricia* dominated below 50 m, followed by *Madracis*, *Undaria*, *Montastraea*, and *Stephanocoenia* (Fig. 7.5). *Agaricia lamarcki*, *A. fragilis*, *A. grahamae*, *M. pharensis*, and *S. intersepta* at 60 m, and *A. undata*, *A. lamarcki*, *A. grahamae*, *M. pharensis*, and *S. intersepta* at >70 m (Fig. 7.6). *A. undata*, *A. lamarcki*, and *A. grahamae* were the main foundation corals within deep MCEs (≥ 50 m), providing three-dimensional structures with medium to large size, sparse, and/or aggregated (shin-

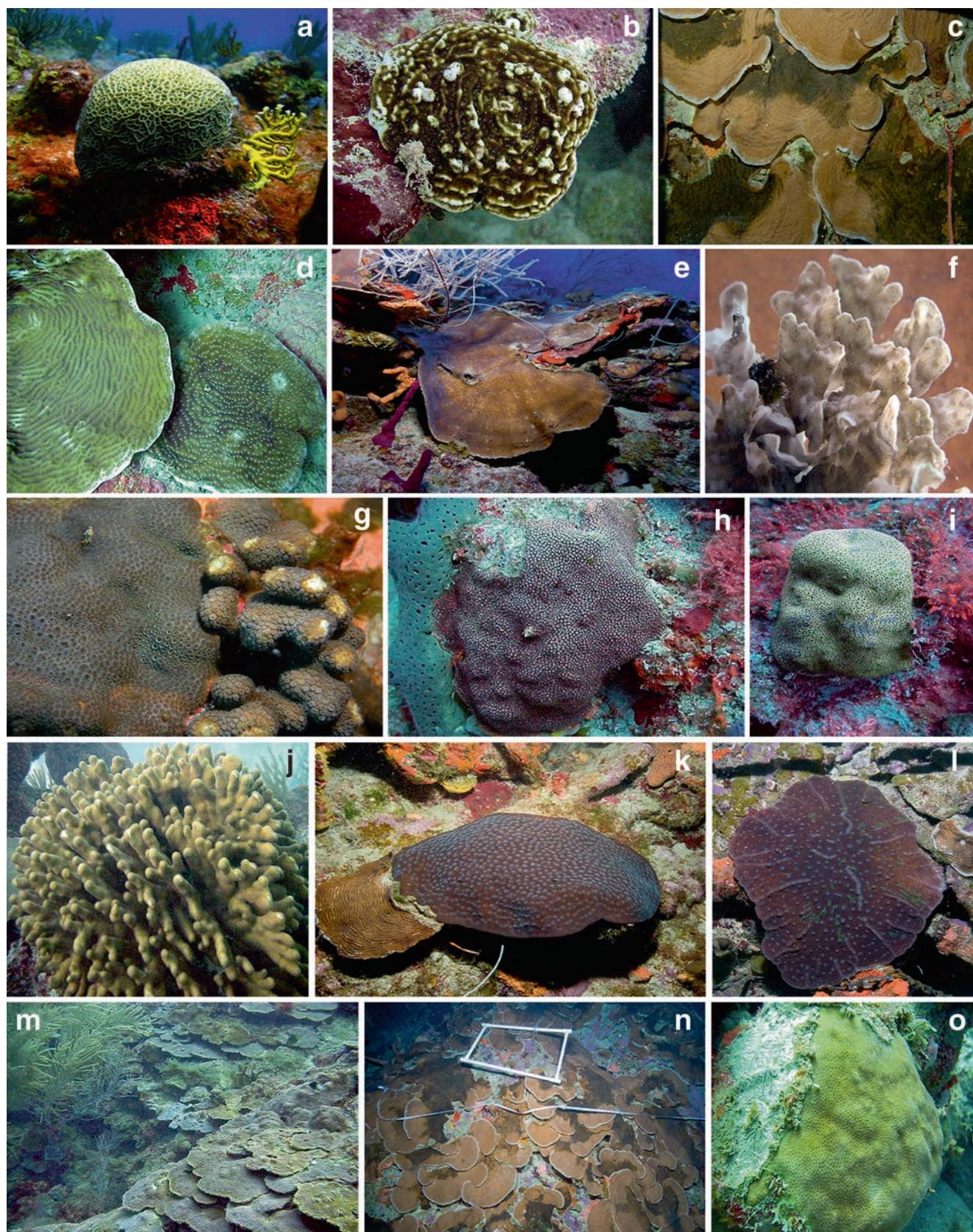


Fig. 7.4 Mesophotic scleractinian species in Puerto Rico. (a) *Undaria agaricites*, (b) *Agaricia fragilis*, (c) *A. undata*, (d, left) *A. grahamae*, (d, right), and (e), *A. lamarckii*, (f) *Leptoseris cailleti*, (g) *Madracis pharensis* (left) and *M. decactis*, (h) *M. pharensis f. pharensis*, (i) *M. pharensis f. luciphila*, (j) *M. formosa*, (k) *Mycetophyllia rissi*, (l) *M. aliciae*, (m) Shingle-like formation of *O. franksi*, (n) *A. undata*, and (o) *Stephanocoenia intersepta*. (Photos credit: E. Weil; except c, e, k, l, n – H. Ruiz, all images can be reused under CC BY license)

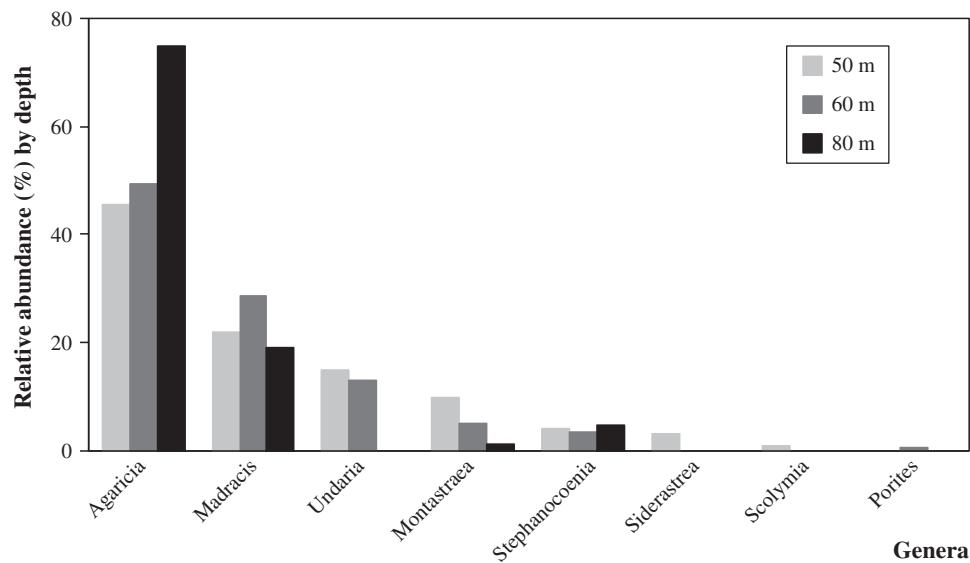


Fig. 7.5 Relative abundance (%) of mesophotic scleractinian coral genera at three depths (50, 60, and 70 m) off southwest Puerto Rico. *Mycetophyllia* and *Leptoseris* were observed but not recorded in photoquadrats. (Weil unpubl. data)

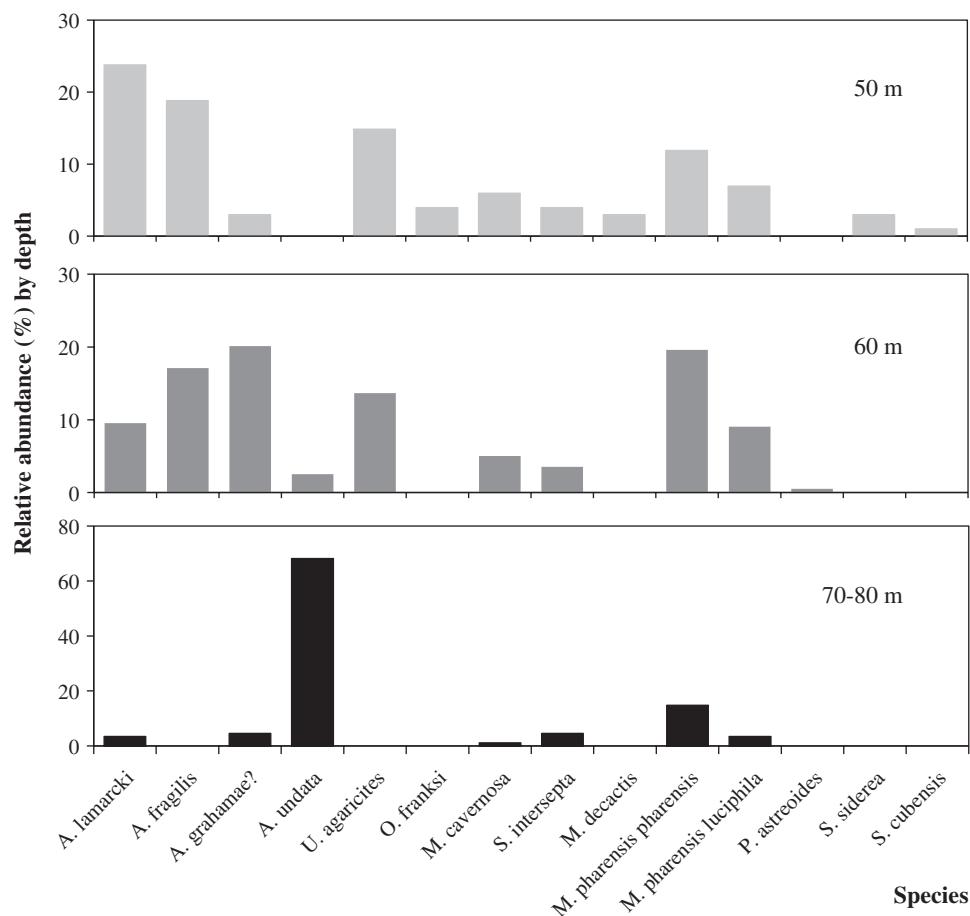


Fig. 7.6 Relative abundances of scleractinian coral species found in random photo-transect surveys at three depths (50, 60, and 70 m) each at two locations off southwest Puerto Rico. “?” = needs verification. (Weil unpubl. data)

gle-like structure) colonies and significantly higher live cover compared to more abundant but smaller colonies of other species. *Orbicella* spp. is the primary group forming the structural framework in mesophotic coral communities above 40 m.

In general, scleractinian diversity, abundance, and cover decline with depth. However, this could vary depending on location, geomorphology, and environmental condition of the area. For example, at the shelf-edge off southwest Puerto Rico, coral cover decreases significantly from 18–20% at 20–25 m to 5–10% at 40–50 m, the lower distribution limits of shallow-water species. Subsequently, coral cover significantly increases to $13.6 \pm 0.4\%$ at 70 m due to the presence of sparse, but large stands of shingle-stacked colonies of the deepwater specialists *A. undata*, *A. grahamae*, and *A. lamarcki* (Ballantine et al. 2008; Weil et al. 2009). Surveys elsewhere in Puerto Rico have shown higher rates of live coral cover, ranging from 29% down to 50 m off Vieques (García-Sais et al. 2004) and >50% at 70 m on Bajo de Sico, an isolated submerged bank in the Mona Channel (Weil unpubl. data).

7.4.3 Fishes

The fish communities within Puerto Rico's MCEs have been surveyed since the 1970s (e.g., Starck and Colin 1978), with exploration expanding recently to cover multiple areas along the south and west coasts (Fig. 7.1), but the most comprehensive survey is that by Bejarano Rodríguez (2013) and Bejarano et al. (2014) that characterized fishes off La Parguera down to 100 m using visual census transects and roving surveys. Over 100 species of fishes were observed at depths >30 m across 31 families (Table 7.3). Mean abundance ranged from 5 to 260 (mean = 56) individuals per 30 m². Species richness ranged from 4 to 16 (mean = 9) species per 30 m². There was no depth-related pattern with species richness, but fish abundance decreased with depth.

Bejarano et al. (2014) divided the fish community within MCEs into species commonly occurring at shallower depths, but extending below 30 m, and those that are primarily distributed below 30 m. The former group constituted 76% of the species observed, and the abundance and frequency of occurrence of most of these decreased rapidly with depth; 34 of these species did not extend below 60 m. Common species within this group are *Stegastes partitus*, *Acanthurus tractus*, and *Sparisoma aurofrenatum*. Most of the other species in this group did not vary significantly with depth, with *Coryphopterus personatus* and *Halichoeres garnoti* being common examples. A few species, such as *Paranthias furcifer*, increased in abundance with depth, but these do not typi-

cally occur inshore of the edge of the platform. The same trend was seen with large predatory fishes, but here refuge with depth from fishing pressure may contribute to this pattern.

The deep group consisted of 26 species (Table 7.3), of which *Chromis insolata* was the most common, representing 23% of all individuals within transects and occurring within 87% of all transects (40–70 m). Other common deep species observed within transects whose density increased with depth include *Liopropoma mowbrayi*, *Lutjanus buccanella*, *Pomacanthus aculeatus*, and *Sparisoma atomarium*. *Xanthichthys ringens* was also common but only down to 60 m. Characteristic, but rare, species include *Serranus chionaraia*, *S. lucioperca*, *Lipogramma klawi*, and *Phaeoptyx pigmentaria*.

The fish assemblage off La Parguera showed a progressive change with depth as shallow species dropped out, and deeper species were documented (Table 7.3). The assemblage at 40 m was distinct from that at 30 m, although they had a greater than 77% similarity. The assemblages at 50 and 60 m combined were distinct from that at 40 m, showing less than a 77% similarity. Characteristic fish species of this deeper depth were *C. insolata* and *L. mowbrayi*. Most distinct was the assemblage at 70 m, with a similarity less than 56% with all other depths. Five species, *Centropyge argi*, *Chromis scotti*, *Haemulon striatum*, *L. buccanella*, and *Prognathodes aculeatus*, best characterized the assemblage at 70 m.

The trophic structure of the mesophotic fish assemblages off La Parguera also changed with depth (Fig. 7.7), a general pattern also noted by García-Sais (2010). Herbivores were the dominant trophic guild at shallow depths, but their proportion declined exponentially with depth. In contrast, the dominant trophic guild at mesophotic depths was that of zooplanktivores, which proportionally increased with depth. At 30 m, zooplanktivores constituted only 16% of the individuals and 21% of the species, while at 60 m their relative abundance and richness were 41% and 60%, respectively. Predators were not well-quantified within transects, but they were frequently observed in roving surveys. At 40–50 m *Lutjanus apodus* was the most abundant predator, but its abundance decreased with increasing depth. Another shallow predator, *Lutjanus jocu*, became dominant at 60 m. In contrast, the mesophotic *L. buccanella*, which first occurred at 60 m, increased in abundance with depth and became the dominant predator by 70 m.

The invasive lionfish, *Pterois volitans*, was infrequently observed off La Parguera down to 70 m. However, its first appearance there was recent, and surveys elsewhere in Puerto Rico, especially along the northwest platform and islands in the Mona Channel, where lionfish first became established,

Table 7.3 Fish species known to inhabit MCEs in Puerto Rico, as reported by Bejarano et al. (2014), with additional literature citations. Bejarano et al. (2014) divided fishes into those historically found in primarily shallow waters and those found at mesophotic depths. Species are sorted by their relative frequency of occurrence from shallow to deep. Depth observed refers to Bejarano et al. (2014), while maximum depth is the maximum reported in the literature.

Species	Common name	Depth (m) observed	Maximum depth (m)	Life stage	Relative frequency of occurrence by depth (m)				
					30	40	50	60	70
Shallow species									
<i>Rhinesomus triqueter</i>	Smooth trunkfish	30–41	50	A	●	●			
<i>Mulloidichthys martinicus</i>	Yellow goatfish	30–36	110	A	●	●			
<i>Canthidermis sufflamen</i>	Ocean triggerfish	41–48	60		nd	●			
<i>Scomberomorus</i> sp.	Mackerel	29–50	55	A	nd	●			
<i>Dasyatis americana</i>	Southern stingray	55	55	A	nd	●			
<i>Elagatis bipinnulata</i>	Rainbow runner	41–52	150	A	nd	●			
<i>Serranus tigrinus</i>	Harlequin bass	30–42	53	A	●	●●			
<i>Acanthurus tractus</i>	Ocean surgeonfish	30–56	56	A	●●●●	●●	●		
<i>Stegastes leucostictus</i>	Beaugregory	30–55	55	A	●●●	●●	●		
<i>Thalassoma bifasciatum</i>	Bluehead wrasse	30–53	53	AJ	●●●●	●●	●		
<i>Holocentrus adscensionis</i>	Squirrelfish	30–53	190	A	●●●			●	
<i>Myripristis jacobus</i>	Blackbar soldierfish	30–62	130	A	●●●	●	●●		
<i>Aulostomus maculatus</i>	Trumpetfish	30–50	50	A	●		●		
<i>Chromis multilineata</i>	Brown chromis	30–50	91	AJ	●		●		
<i>Sparisoma viride</i>	Stoplight parrotfish	30–60	60	A	●●●		●		●
<i>Acanthurus chirurgus</i>	Doctorfish	30–60	60	A	●●●		●●		●
<i>Acanthurus coeruleus</i>	Blue tang	30–60	61	A	●●	●	●		●
<i>Coryphopterus lipernes</i>	Peppermint goby	30–60	60	A	●●	●	●		●
<i>Haemulon sciurus</i>	Bluestriped grunt	30–60	60	A	●●	●	●		●
<i>Caranx ruber</i>	Bar jack	30–61	91	AJ	●●		●		●
<i>Anisotremus virginicus</i>	Porkfish	30–61	61	A	●●	●	●		●
<i>Scarus iseri</i>	Striped parrotfish	30–60	60	J	●●				●
<i>Lutjanus apodus</i>	Schoolmaster	29–70	70	AA	●●	●●	●		●
<i>Bodianus rufus</i>	Spanish hogfish	30–60	70		●		●		●
<i>Holacanthus ciliaris</i>	Queen angelfish	30–61	82	A	●	●	●		●
<i>Epinephelus guttatus</i>	Red hind	30–64	100	A	●	●	●		●
<i>Lutjanus mahogoni</i>	Mahogany snapper	30–60	100	AA	●		●		●●
<i>Haemulon flavolineatum</i>	French grunt	30–70	70	A	●●●	●●	●		●
<i>Stegastes partitus</i>	Bicolor damselfish	30–70	116	AJ	●●●●●	●●●●	●●●	●	●
<i>Sparisoma aurofrenatum</i>	Redband parrotfish	30–70	70	AJ	●●●●	●●	●●	●●	●
<i>Ocyurus chrysurus</i>	Yellowtail snapper	30–70	180	AJ	●●●	●●	●●	●	●
<i>Clepticus parrae</i>	Creole wrasse	30–80	190	AJ	●●●	●●	●●	●	●
<i>Chaetodon capistratus</i>	Foureye butterflyfish	30–74	91	AJ	●●●	●●	●●●	●●	●
<i>Gramma loreto</i>	Fairy basslet	30–70	70		●●●	●●●	●●	●●	●
<i>Scarus taeniopterus</i>	Princess parrotfish	30–70	70	AJ	●●●●	●●●	●●●	●●●	●●
<i>Chromis cyanus</i>	Blue chromis	30–70	70	AJ	●●●●	●●●●	●●●●	●●	●●
<i>Pterois volitans</i>	Lionfish	30–70	70	AJ	●●	●●	●	●●	●
<i>Coryphopterus personatus</i>	Masked goby	30–70	70	AJ	●●●●	●●●●	●●●●	●●●●	●●
<i>Elacatinus evelynae</i>	Sharknose goby	30–74	74	AJ	●●	●●	●●	●●	●
<i>Canthigaster rostrata</i>	Sharpnose puffer	30–70	160	J	●●	●●	●●	●●	●

(continued)

Table 7.3 (continued)

Species	Common name	Depth (m) observed	Maximum depth (m)	Life stage	Relative frequency of occurrence by depth (m)				
					30	40	50	60	70
<i>Ophioblennius macclurei</i>	Redlip blenny	30–70	70	A	●			●	●
<i>Haemulon plumieri</i>	White grunt	30–70	70	A	●	●	●	●	●
<i>Hypoplectrus chlorurus</i>	Yellowtail hamlet	30–74	74	A	●	●	●		●
<i>Lachnolaimus maximus</i>	Hogfish	30–67	67	A	nd	●	●	●	●
<i>Mycteroperca bonaci</i>	Black grouper	41–91	91	AA	nd	●	●	●	●
<i>Carcharhinus perezii</i>	Reef shark	48–91	91	AA	nd	●	●	●	●
<i>Halichoeres garnoti</i>	Yellowhead wrasse	30–80	90	AJ	●●●●	●●●●	●●●●	●●●●	●●●●
<i>Cephalopholis cruentata</i>	Graysby	30–80	170	AJ	●●●●	●●●●	●●●●	●●●●	●●●●
<i>Pomacanthus paru</i>	French angelfish	30–70	100	A	●		●		●
<i>Sphyraena barracuda</i>	Great barracuda	30–73	110	A	●	●	●	●	●
<i>Rypticus saponaceus</i>	Greater soapfish	30–70	140	A	●	●	●	●	●
<i>Cephalopholis fulva</i>	Coney	30–70	216	AJ	●	●	●	●	●
<i>Balistes vetula</i>	Queen triggerfish	30–71	275		●	●	●	●	●
<i>Anisotremus surinamensis</i>	Black margate	30–67	67	A	nd	●			●
<i>Scarus guacamaia</i>	Rainbow parrotfish	71	71	A	nd	●			●
<i>Caranx latus</i>	Horse-eye jack	73	140	A	nd	●			●
<i>Hypoplectrus</i> sp.	Hamlet	60–70	70		●			●	●
<i>Holocentrus rufus</i>	Longspine squirrelfish	30–70	216	A	●●	●●	●●●	●●	●●
<i>Lutjanus analis</i>	Mutton snapper	48–91	170	AA	●	●	●●	●●	●
<i>Lutjanus jocu</i>	Dog snapper	40–74	74	AA	nd	●●●●	●●●●	●●●●	●●●●
<i>Neoniphon mariannus</i>	Longjaw squirrelfish	30–70	91	A	●●●●	●●●●	●●●●	●●●●	●●●●
<i>Coryphopterus glaucofraenum</i>	Bridled goby	40–61	61	A		●	●	●	●
<i>Lutjanus cyanopterus</i>	Cubera snapper	40–73	73	AA	nd	●●	●●	●	●●
<i>Caranx lugubris</i>	Black jack	52–91	364	A		●●	●●	●	●●
<i>Pomacanthus arcuatus</i>	Gray angelfish	40–73	91	A		●	●	●	●●
<i>Paranthias furcifer</i>	Creole fish	50–70	190	AJ			●	●	●●
<i>Epinephelus itajara</i>	Goliath grouper	55	100	A	nd		●		
<i>Synodus intermedius</i>	Sand diver	50	320	A			●		
<i>Mycteroperca venenosa</i>	Yellowfin grouper	41–45	137	A					
<i>Hypoplectrus puella</i>	Barred hamlet	50–70	70	A			●		●
<i>Muraena retifera</i>	Reticulate moray	65–70	76	A				●	
<i>Sphyraena</i> sp.	Hammerhead shark	61	80	A	nd			●	
<i>Stegastes variabilis</i>	Cocoa damselfish	60	190	A				●	
<i>Calamus penna</i>	Sheepshead porgy	61	87	AJ				●	
<i>Ginglymostoma cirratum</i>	Nurse shark	58	130	A	nd			●	
<i>Holacanthus tricolor</i>	Rock beauty	60–70	135	A				●	●
<i>Chaetodon ocellatus</i>	Spotfin butterflyfish	70	70	A					●
<i>Trachinotus falcatus</i>	Permit	91	130	A					
Deep species									
<i>Serranus</i> sp.	Bass	40	130			●			
<i>Chaetodon sedentarius</i>	Reef butterflyfish	30–70	105		●	●		●	●

(continued)

Table 7.3 (continued)

Species	Common name	Depth (m) observed	Maximum depth (m)	Life stage	Relative frequency of occurrence by depth (m)				
					30	40	50	60	70
<i>Phaeoptyx pigmentaria</i>	Dusky cardinalfish	70	70	nd	●				●
<i>Serranus luciopercaurus</i>	Crosshatch basslet	70	190	nd	●				●
<i>Serranus annularis</i>	Orangeback bass	39–82	82		●				●
<i>Serranus tabacarius</i>	Tobaccofish	40–70	190		●	●		●	●
<i>Serranus tortugarum</i>	Chalk bass	40–70	396		●●	●	●●	●●	●●
<i>Sparisoma atomarium</i>	Greenblotch parrotfish	40–73	106		●●	●●	●●	●●	●●
<i>Xanthichthys ringens</i>	Sargassum triggerfish	40–70	190		●●	●●●	●●●	●●	●●
<i>Chromis insolata</i>	Sunshinefish	30–80	152		●●	●●●●	●●●●●	●●●●●	●●●●●
<i>Prognathodes aculeatus</i>	Longsnout butterflyfish	30–79	145		●		●●	●●	●●●●
<i>Centropyge argi</i>	Cherubfish	40–80	106		●			●●	●●●
<i>Chromis scotti</i>	Purple reef fish	30–80	120		●	●	●●	●●●	
<i>Liopropoma mowbrayi</i>	Cave bass	40–70	130		●	●●	●●●	●●●●	
<i>Apogon lachneri</i>	Whitestar cardinalfish	50–82	106				●		
<i>Halichoeres cyancephalus</i>	Yellowcheek wrasse	52–70	91			●			●
<i>Liopropoma rubre</i>	Peppermint bass	50–70	70			●		●	●
Apogon sp.	Cardinalfish	42–60	273	nd				●	
<i>Gramma</i> sp.	Basslet	60–64	130				●		
<i>Liopropoma carmabi</i>	Candy basslet	61	70				●		
<i>Serranus chionaraia</i>	Snow basslet	60	90						
<i>Liopropoma</i> sp.	Bass	60–70	70				●	●	
<i>Lutjanus buccanella</i>	Blackfin snapper	52–91	273				●●●	●●●●	
<i>Serranus luciopercaurus</i>	Crosshatch basslet	70	190					●	
<i>Lipogramma klayi</i>	Bicolor basslet	80	145						
<i>Haemulon striatum</i>	Striped grunt	70–91	210					●	
Other species reported at mesophotic depths									
<i>Aeobatis narinari</i>	Spotted eagle ray								
<i>Amblycirrhitus pinos</i>	Redspotted hawkfish								
<i>Decapterus macarellus</i>	Mackerel scad								
<i>Hypoplectrus indigo</i>	Indigo hamlet								
<i>Hypoplectrus unicolor</i>	Butter hamlet								
<i>Kyphosus sectatrix</i>	Bermuda chub								
<i>Negaprion brevirostris</i>	Lemon shark								
<i>Scomberomorus cavalla</i>	King mackerel								
<i>Seriola rivoliana</i>	Almaco jack								
<i>Antilligobius nikkae</i>	Saber goby		91						
<i>Gramma linki</i>	Yellowlined basslet		30, 90–130						
<i>Lipogramma regium</i>	Royal basslet		70–75						

Life stage: A adult, J juvenile, nd not determined

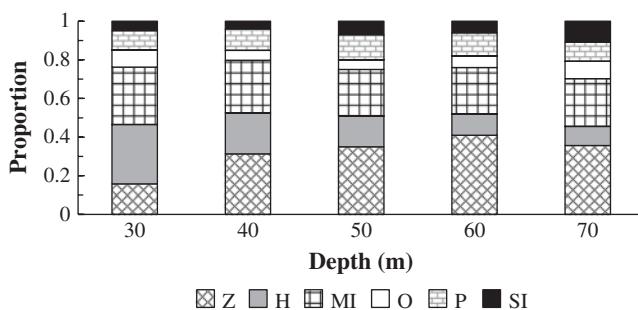


Fig. 7.7 Mean trophic guild proportions (relative density) observed in 30 m² transects from a 20 to 70 m depth gradient off La Parguera, Puerto Rico. Z, zooplanktivore; MI, mobile invertebrate feeder; H, herbivore; O, omnivore; P, piscivore; and SI, sessile invertebrate feeder. (Modified from Bejarano et al. 2014)

showed them to be abundant at mesophotic depths, occurring at depths exceeding 100 m.

7.4.4 Other Biotic Components

The majority of past studies along the PR-VI platform have concentrated on the macrofauna and macroflora to reveal widely distributed MCEs, yet a true estimation of biodiversity compared to shallow-water reefs is lacking (Kahng et al. 2010). In particular, the mesophotic zone may be a biodiversity hotspot inhabited by a transitional cryptic fauna (Petrescu et al. 2013), arguably the most diverse metazoan taxa of the reefs. Cryptic meiotauna and small macrofauna (0.125–1 mm) associated with MCE substrata (e.g., sediments, loose rubble, corals, sponges, macroalgae, and rhodoliths) were characterized from several sites across the PR-VI platform, including those off La Parguera (Sherman et al. 2013).

From these qualitative samples, macrofauna and meiotauna taxa ($n = 21,551$) were counted and separated into Orders as the lowest taxonomic level. Several taxonomic studies have been published on new species of cumaceans, amphipods, harpacticoid copepods, and mites of the MCEs of Puerto Rico (Petrescu et al. 2016 and references therein). Here, we report trends in numerical dominance and diversity of the major macrofauna and meiotauna taxa.

A total of 12 benthic taxonomic groups were identified, with counts per location/depth ranging from 1714 to 3420 individuals (Fig. 7.8). The highest abundances were found in the deeper MCE samples (> 50 m), followed by intermediate depth reefs (<50 m). The samples with the highest number of organisms were El Seco, Vieques ($n = 6719$), followed by North Buoy 8 (western Puerto Rico; $n = 4474$); both samples were deeper than 50 m (Fig. 7.8). In every location, irrespective of depth, copepods were the numerically dominant taxon ($n = 14,791$) of the total benthic community, with a relative abundance higher than 53%. Amphipods represented the sec-

ond most abundant assemblage ($n = 1865$), with 15.6% relative abundance at the deeper reefs (>50 m). The third most abundant assemblage was the ostracods ($n = 1563$), with most of specimens found in El Seco, Vieques ($n = 1304$). Tanaids ($n = 1262$), halacarid mites ($n = 868$), isopods ($n = 771$), and cumaceans ($n = 176$) were also more abundant in deeper than intermediate depth reefs (Fig. 7.8; Schizas unpubl. data). Other abundant taxa (e.g., polychaetes and nematodes) were not analyzed. In general, there was great variability in the number of specimens at each location, with the deeper mesophotic samples (>50 m) yielding more specimens than the intermediate depth mesophotic samples (<50 m). Higher-resolution taxonomic studies are necessary before depth stratification of cryptic fauna can be assessed.

7.5 Ecology

The strong influence of geomorphology on MCE development is illustrated by comparing two locations (HW and EH) on the upper slope off of La Parguera. HW has a steep gradient (~44°, Fig. 7.3) and rugose topography consisting of steep-sided buttresses separated by narrow sand chutes. These buttresses support a lush benthic cover (Fig. 7.9, left). In contrast, EH has a gentler gradient of ~25° (Fig. 7.3) and lower rugosity, with the substratum consisting of sparsely colonized hard ground supporting lower coral cover and thin, discontinuous sheets of unconsolidated sand (Fig. 7.9, right). Differences in species richness and dominant taxa led to significant differences in community structure between sites, which is evident at both 50 and 70 m depth (Fig. 7.10; Sherman et al. 2010). Overall, little difference was seen in total algal cover and open sand across sites, but coral (11.7%) and sponge (15.3%) cover at HW were greater than at EH (6.3% and 10.1%, respectively).

Seventy-five algal species were identified from both EH and HW. Surprisingly, only slightly more than a third of the species were common to both sites. EH hosted 81% of these species and 59% at HW (i.e., the EH algal diversity was roughly 30% greater than at HW). With respect to depth, 55% of the combined species were found deeper at EH than at HW (where 27% of the species attained deeper depth distributions).

At HW there were ten algal taxa at 50 m, dominated by *Dictyota* sp. (16.2%), *Lobophora variegata* (11.6%), coralline algae (8.1%), and *Schizothrix* sp. (5.6%). There were 11 coral species at 50 m, with *A. lamarki* dominant at 2.7% cover. EH had a higher algal richness (12 taxa), with *Schizothrix* sp. (15.7%), *Dictyota* sp. (13.2%), and coralline algae (6.7%) being dominant. However, coral richness (4) was much lower and was dominated by *A. undata* (3.85%). At 70 m, HW had nine algal species, dominated by coralline algae (12.5%), *Peyssonnelia* sp. (9.2%), *P. gigaspora* (4.5%),

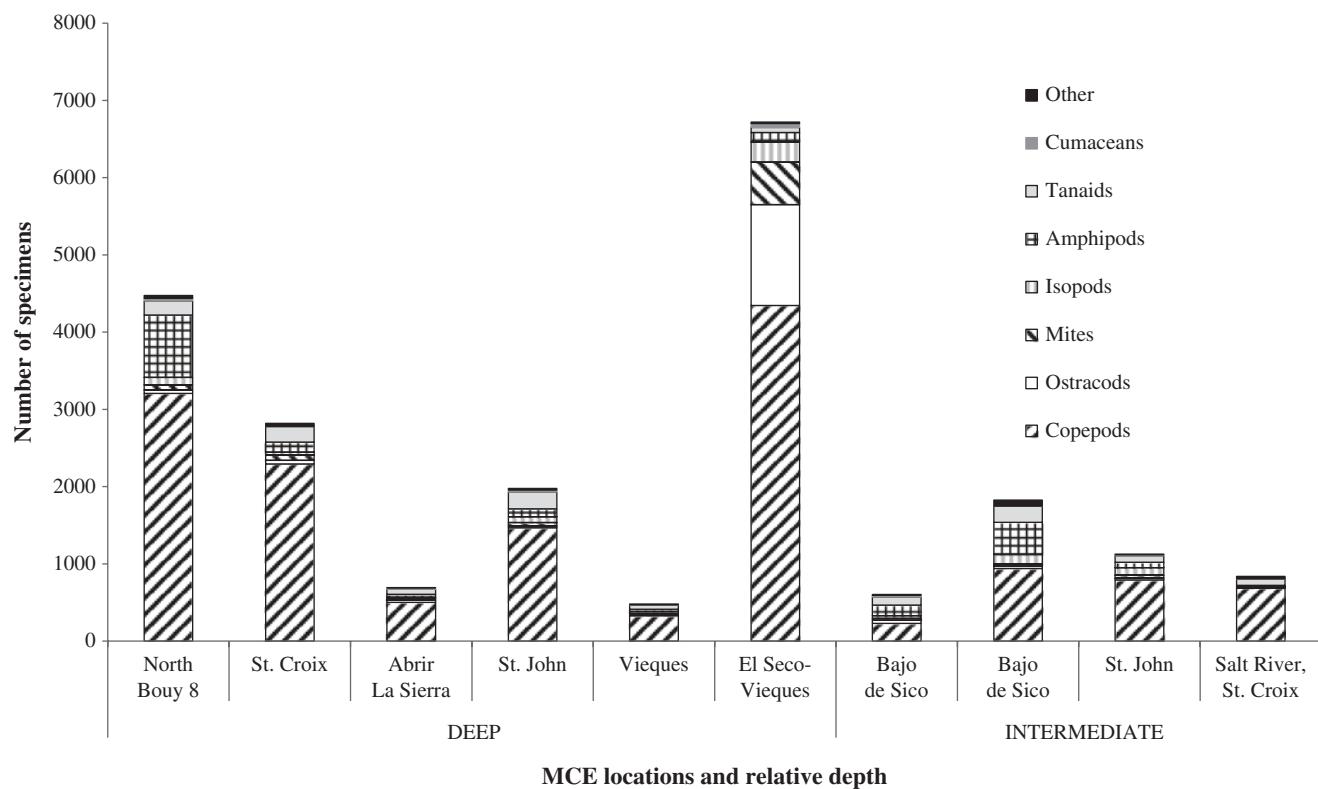


Fig. 7.8 Composite of macrofauna and meiofauna taxa from MCEs of Puerto Rico and the US Virgin Islands. Locations shown twice indicate different sampling dates. (Schizas, unpubl. data)



Fig. 7.9 Photographs illustrating the geomorphology and benthic communities on southwest (left) and southeast (right) facing slopes of La Parguera, Puerto Rico (Photo credits: H. Ruiz, can be reused under CC BY license)

and *Dictyota* (4.1%), and six coral species, with *A. undata* overwhelmingly dominant (13.3%). In contrast, EH had 13 algal taxa, dominated by *Dictyota* sp. (9.7%), *Schizothrix* sp. (7.5%), and coralline algae (7.5%), and 13 species of coral (8.5% total), again dominated by *A. undata* (6.1%).

Over a broader range of sites off La Parguera, Bejarano Rodríguez (2013) found higher species richness and double

the overall fish abundance at physically complex sites. Common species characteristic of high complexity sites are *Coryphopterus personatus*, *Elacatinus evelynae*, and *Gramma loreto*. Higher abundances were driven by differences within zooplanktivores and piscivores, including *Ocyurus chrysurus*, *L. jocu*, *L. cyanopterus*, *L. apodus*, *Cephalopholis cinctata*, and *Mycteroperca bonaci*.

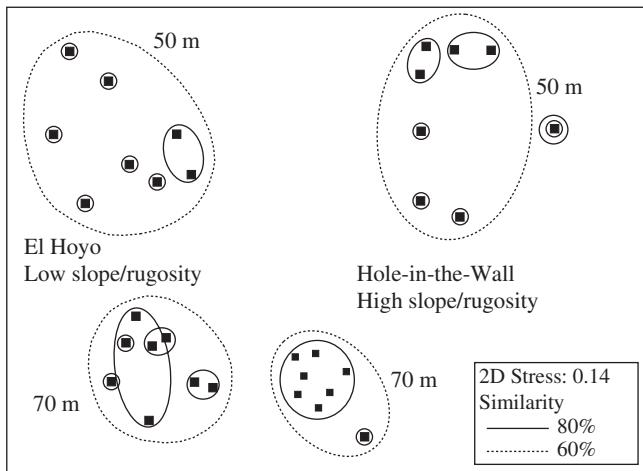


Fig. 7.10 Nonmetric multidimensional scaling (MDS) ordination comparing two sites, EH and HW, at 50 and 70 m along the insular slope off La Parguera, Puerto Rico (Data were % cover taken from replicate $12 \times 0.4\text{ m}$ (4.8 m^2) high-resolution photo-transect surveys at each site and depth (Ruiz unpubl. data))

Additionally, rare large-bodied species (*Mycteroperca venenosa*, *Epinephelus itajara*, *Scarus guacamaia*, *Canthidermis sufflamen*, and *Dasyatis americana*) were only at high complexity sites. The only species more abundant at low complexity sites was *Xanthichthys ringens*.

There is a distinct transition with depth across benthic taxa (Fig. 7.10), individually for corals, algae, and fishes. In general, community composition at shallow mesophotic depths (30–40 m) is similar to that of shallow reefs, but by 50 m the overall MCE community shows a distinct change from shallower depths, while another distinct break occurs between 50 and 70 m across all taxa. Nevertheless, these changes in community composition with depth occur through the gradual decline of shallower species and the increase in abundance of deeper species (Tables 7.1, 7.2, and 7.3).

The sharper changes in community composition can be related to changes in geomorphology, light levels, and in part decreasing herbivore abundance with depth. Below 60 m, calcified algae become dominant. The decline in herbivores may be related to this increase in cover of calcified Peyssonneliaceae and coralline algae (Fig. 7.11) as these species possess low nutritional value, as well as lower palatability as a consequence of calcification. Success by coralline algae at depth may be related to lower competition for space with coral species and by decreased macroalgal shading. The crustose coralline species have higher surface-to-volume ratios, enhancing light capture, despite the lower irradiance levels, relative to their macroscopic algal counterparts. Below 60 m, brown algae of the genus *Lobophora* transitioned from foliose to the encrusting *L. littlerorum* (Bejarano et al. 2014). In corals, *A. undata* becomes the dominant species, forming large monospecific stands of plate-like colonies in some areas. Only small-bodied herbivorous fishes (e.g., *Sparisoma atomarium* and *Centropyge argi*)

had their maximum occurrence below 60 m, reflecting the reduced competition from larger species, while still being able to meet their lower metabolic demands despite reduced abundance of non-calcified algae (Bejarano et al. 2014). The most prominent impact of geomorphology is the abrupt change of inclination at approximately 90 m, below which a wall environment exists that supports little benthic cover.

As herbivorous fishes decline, zooplanktivores become the dominant fish trophic group. Other trophic groups do not proportionally increase as herbivores decline. Thus, the increase in zooplanktivores is thought to be driven not only by the decline in benthic algal availability but also by the greater availability of nutrients and particulate matter that may be imported from rich deep waters to mesophotic depths by observed upwelling and internal waves. Higher nutrient levels at the base of the thermocline support higher primary production and the formation of the chlorophyll maximum (mean from 76 to 95 m off southwest Puerto Rico; Corredor and Morell 2001). These may provide the main energy source in lower mesophotic habitats (Lesser and Slattery 2013); thus, favoring planktivores and filter feeders (e.g., the shift of *Madracis pharensis luciphila* to *M. pharensis pharensis* with depth; Sherman et al. 2010).

The degree of connectivity among mesophotic and shallow scleractinian corals in Puerto Rico is not well studied. On a community basis, the dominant species at 50 m and below are significantly different than those found in shallow reefs, suggesting little connectivity. Even for species that are distributed broadly across the full mesophotic depth range, such as *M. cavernosa*, the functional degree of connectivity is questionable given that mesophotic colonies are usually small and widely scattered, suggesting limited reproductive potential. Genetic studies have only investigated the population structure of *A. lamarki* off southwest Puerto Rico and only down to 40 m depth; no vertical or horizontal population structure was found, indicating complete mixing between shallow and the upper most mesophotic depths (Hammerman et al. 2018), despite a depth stratification observed in the *Symbiodinium* hosted by *A. lamarki* (Lucas et al. 2016).

In contrast, the evidence suggests a high degree of vertical connectivity within fishes. In Table 7.3, 75% of the species observed within mesophotic depths represent shallow species. Bejarano Rodríguez (2013) found just two species (*Scarus iseri* and *Canthigaster rostrata*) with only juveniles at mesophotic depths. Most species showed either a mixture of adults and juveniles across shallow and mesophotic reefs or evidence of potential ontogenetic migration from shallow to mesophotic depths, including 22 species (e.g., snappers, grunts, surgeonfishes, and barracuda) common at mesophotic depths but known to use nearshore nursery habitats (e.g., seagrass, mangroves, and shallow backreef; but see McMahon et al. 2016).

Temporal variability in benthic species, assessed over a full year at 3-month sampling intervals at both HW and EH,

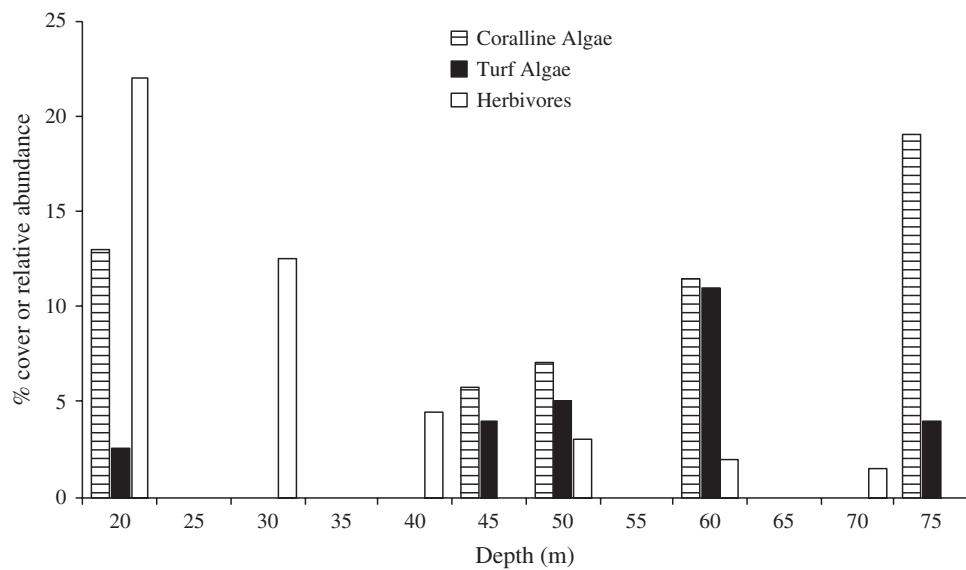


Fig. 7.11 Mean cover (%) of coralline algae, turf algae, and relative density (%) of herbivorous fishes per depth, along a gradient from 20 to 70 m at six reefs in La Parguera shelf-edge, southwest Puerto Rico. (From Bejarano et al. 2014)

tended to be low, with trends being similar across sites and depths (Appeldoorn et al. 2016c). Dominant changes occurred among the macroalgae, particularly *Dictyota* and *Schizothrix*, with the former oscillating from near 0 to over 30% cover, peaking in March and September. The latter species showed a general increase over time. There is a general reduction in the degree and magnitude of community variability observed from 30 to 70 m. Contrary to the algal community, there was no significant temporal variability in composition (biodiversity), relative abundances (%), and live cover of scleractinian species. The most abundant species, *M. pharensis*, lost eight colonies (out of 70=11% mortality) at 50 m at HW compared to five colonies (out of 24=27% mortality) at EH at the same depth. However, overall abundances were only reduced by an average of 6% at 50 m over 1 year. As most of these colonies were small juveniles or recruits that were apparently smothered by algal overgrowth, live coral cover (%) varied little over time.

One clear example of disease progression and mortality was observed. Between September and December of 2009, a medium-sized colony of the platy *M. aliciae* at HW showed signs similar to white plague disease found in shallow reefs. The colony died completely in less than 3 months (Andradi-Brown et al. 2016; Weil 2019).

7.6 Threats and Conservation Issues

In Puerto Rico, MCEs are subject to the same array of threats affecting shallow reefs. Global stressors include warming, which can lead to disease outbreaks and bleaching, and acidification (Andradi-Brown et al. 2016; Weil 2019). Local threats

include overfishing (Appeldoorn et al. 2015) and invasive species (e.g., Toledo-Hernandez et al. 2014; Ruiz et al. 2017), which threaten to alter trophic pathways, especially those that may alter the degree of herbivory and algal cover (e.g., Lesser and Slattery 2011). The presence of sharks and of large and medium-bodied snappers, groupers, and parrotfishes within MCEs suggests these systems likely play a key conservation role for shallow fishes threatened by overfishing, which have markedly declined in abundance (Appeldoorn et al. 2016b). For example, in La Parguera these fishes were once reported to be common in the area (Kimmel 1985) but have since become rare and uncommon in shallow habitats (Pittman et al. 2010). Bejarano-Rodríguez (2013) found large-bodied species to be more abundant between 50 and 70 m depth. Sighting frequencies of Cubera and dog snappers, black grouper, and sharks increased with depth and were maximum at 70 m, suggesting that deep MCEs already serve as refugia for these fishes.

Although MCEs are located along the insular shelf-edge and slope, Puerto Rico's narrow shelf means MCEs are still susceptible to terrestrial sources of sedimentation and turbidity, either from direct anthropogenic activities or poor land use practices. Appeldoorn et al. (2016a) documented severe siltation within MCEs off Ponce on the south coast, an area affected by river runoff, port activities, coastal development, and offshore dredge disposal. Currently, there are ten regional wastewater treatment plants in Puerto Rico, accounting for 95% of all sewage discharge, all with at least primary treatment. While most of these discharge into shallow coastal waters, some outfalls are in the upper mesophotic zone (e.g., 43 m: Puerto Nuevo, Bayamon), where changes in the depth of the thermocline due to internal waves will actively disperse the effluent throughout the mesophotic zone. Other sites (e.g.,

Ponce, Mayagüez) consist of deep outfalls discharging primary treated effluent at lower mesophotic depths and deeper. For example, while the base of the Ponce outfall is located at 125 m, the design criteria was to contain the discharge plume to depths no shallower than 36 m. Deep sewage outfalls can impact MCEs in two ways. First, they are a high source of nutrients, pathogens, and potentially contaminants. Increased nutrients can lead to eutrophication and subsequent plankton growth and greater turbidity, while pathogens have been implicated in the spread of coral diseases (Sutherland et al. 2011). Second, substantial substratum destruction can occur when the outfalls are buried by backfill, such as occurred in Ponce to a depth of over 55 m, with little colonization observed after 11 years of operation.

As with shallow coral ecosystems, MCEs are patchily distributed, depending on geomorphology and sediment dynamics, and are an oasis of biodiversity both within benthic communities and the fish assemblages they support, including species of high conservation value, such as turtles and sharks. Thus, MCEs should be protected on a scale equal to that afforded to shallow reefs. Marine protected areas (MPAs) are one method to afford protection to MCEs, but such MPAs should be designed to incorporate and protect the assumed high degree of reef fish connectivity between shallow reef habitats and MCEs. Schärer et al. (2014) documented 29 MPAs in Puerto Rico. Of these, half extended across the shelf to include the insular slope, but almost all of these have no management plans or any degree of regulation within the marine environment. Only two MPAs (Mona Island and Desecheo Island) are both true marine reserves and cover the full range of habitats from the shoreline to beyond mesophotic depths. While few surveys exist to confirm the existence of well-developed MCEs within existing MPAs (e.g., García-Sais 2010; García-Sais et al. 2004, 2010, 2011, 2012), the correlation between slope geomorphology and MCE distribution provides a degree of predictability for MPA design purposes.

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