Coral Reefs (2010) 29:347–360
DOI 10.1007/s00338-010-0607-4

REPORT

Geomorphology and benthic cover of mesophotic coral ecosystems of the upper insular slope of southwest Puerto Rico

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Received: 30 March 2009 / Accepted: 19 February 2010 / Published online: 7 March 2010

Abstract The upper insular slope of southwest Puerto Rico is defined as extending from the shelf break at ~20 m water depth down to a depth of ~160 m where there is a pronounced change in geomorphic character and the basal slope begins. The upper slope is divided into two geomorphic zones separated by a pronounced break in slope gradient at ~90 m water depth. Descending from the shelf break, these are Zone I (20–90 m) and Zone II (90–160 m). As orientation of the shelf margin changes, geomorphology of Zone I shows systematic variations consistent with changes in exposure to prevailing waves. Within Zone I, exposed southeast-facing slopes have a gentler gradient and lower relief than more sheltered southwest-facing slopes, which are steep and irregular. Mesophotic coral ecosystems (MCEs) are largely restricted to Zone I and concentrated on topographic highs removed from the influence of active downslope sediment transport. Accordingly, MCEs are more abundant, extensive and diverse on southwest-facing slopes where irregular topography funnels downslope sediment transport into steep narrow grooves. MCEs are more sporadic and widely spaced on southeast-facing slopes where topographic highs are more widely spaced and downslope sediment transport is spread over open, low-relief slopes inhibiting coral recruitment and growth. Relict features formed during preexisting sea levels lower than present include deep buttresses at ~45–65 m water depth and a prominent terrace at ~80 m. Based on correlations with existing reef accretion and sea-level records, it is proposed that the 80-m terrace formed during the last deglaciation ~14–15 ka and subsequently drowned during a period of rapid sea-level rise associated with meltwater pulse 1A at ~14 ka and deep buttresses at ~45–65 m formed between ~11.5 and 13.5 ka and then drowned during a period of rapid sea-level rise associated with meltwater pulse 1B at ~11.3 ka.

Keywords Insular slope · Geomorphology · Mesophotic coral ecosystem · Relict reef · Puerto Rico

Introduction

Upper insular and continental slopes of the Caribbean are regions of special interest for several reasons. In particular, these areas are prime habitats for mesophotic coral ecosystems (MCEs) and they contain relict topographic features that represent important geological archives of late Quaternary sea-level and climate change. MCEs are characterized by the presence of light-dependent corals and associated communities that are typically found at depths starting at 30–40 m and extending to over 150 m in tropical and subtropical regions. The dominant communities providing structural habitat in the mesophotic zone can be comprised of coral, sponge and algal species (Hinderstein et al. 2010). There is renewed interest in these ecosystems as, being further removed from terrestrial and anthropogenic influences than shallower environments (e.g., Armstrong et al. 2006), they may serve as refugia for corals and other species during times of environmental stress and a possible source of larvae that could boost the resiliency of shallower reefs (Riegl and Piller 2003; Lesser et al. 2009; Bongaerts et al. 2010). In addition, the potentially large

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Communicated by Guest Editor Dr. John Marr

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areal extant of MCEs rivals that of shallow reef systems (Locker et al. 2010).

Relict ridges and terraces have been identified on the slopes of several locales around the Caribbean including Barbados (Macintyre et al. 1991), the west and southwest coast of Puerto Rico (Seiglie 1971), western Guiana and the north coast of Jamaica (Macintyre et al. 1991; Macintyre 2007; and references therein). Coring of a series of submerged ridges on the south coast of Barbados showed that these structures are relict shallow-water reefs formed during previous sea levels lower than present. Radiometric dating and interpretation of these records have provided critical information on sea-level and other oceanographic and climatic change during the last deglaciation (Fairbanks 1989; Bard et al. 1990). Investigations of relict reef structures on slopes in regions such as Hawaii (Webster et al. 2004b, 2006), Papua New Guinea (Webster et al. 2004a), the Marquesas (Cabioch et al. 2008) and Tahiti (Camoin et al. 2006; Expedition 310 Scientists 2007) have confirmed the importance of these features as geological archives of oceanographic and climatic change. In addition, relict reefs provide a unique paleoecological record of the response of reef ecosystems to environmental changes. Relict reefs are generally well lithified, topographically high features and, therefore, can represent important habitats for MCEs. Macintyre et al. (1991) describe a rich cover of sponges, algae and scattered corals atop a relict reef at a depth of ~70 m off the west coast of Barbados. Thus, upper slope environments represent both unique coral habitats as well as important geological and paleoecological archives that are especially relevant during the current era of rapid environmental change.

Compared to their shallower counterparts, MCEs have received limited study in Puerto Rico and the U.S. Virgin Islands. Only recently have technologies such as ROVs, AUVs and technical diving techniques have been specifically focused on studying these systems (cf. Locker et al. 2010). MCEs have been described off the south coast of Vieques, on the insular slope of Isla Desecheo, at Bajo de Sico seamount in the Mona Passage (Garcia-Sais et al. 2005, 2007, 2008) and on the broad insular shelf that stretches south of St. Thomas and St. John (Armstrong et al. 2006). These deep hermatypic coral formations have been divided into three types including deep terrace/deep insular shelf reefs, drop-off wall reefs and rhodolith reefs. Locker et al. (2010) provide a summary of the geomorphology of these different settings. Thus far, MCE research in Puerto Rico and USVI has focused on environments at depths of ~30–50 m. Only limited information exists on deeper MCEs at depths of 50–100 m. The current study represents some of the first in situ observations and descriptions of these deeper settings in Puerto Rico and USVI.

A first step in understanding both MCEs as well as the history of relict features of the upper slope is a characterization of their composition, distribution and general physical setting in which they occur. With this information, relationships can be established between these different factors that improve our understanding of these systems as well as help to direct future studies. The objectives of this study are to: (1) describe the geomorphology of the upper insular slope of southwest Puerto Rico; (2) identify geomorphic features and breaks in slope that occur at consistent depths among different sites; (3) characterize the macrobenthic cover at selected sites; and (4) describe the interrelationships between slope geomorphology, sea-level change and MCEs.

Materials and methods

The study area (Fig. 1) lies off the southwest coast of Puerto Rico where a broad shelf extends ~8 km offshore before dropping abruptly to oceanic depths. This research focused on a ~12-km section of the upper insular slope. For this locale, the upper slope is herein defined as the zone from the shelf break at a water depth of ~20 m down to a depth of ~160 m where there is a pronounced change in geomorphic character and the basal slope begins. The basal slope refers to the zone of the insular slope beyond ~160 m water depth. The depth range of the upper insular slope (20–160 m) encompasses the range of MCEs as well as glacio-eustatic lowstands during the late Quaternary. Multibeam bathymetry for the region was obtained from a hydrographic survey conducted in 2006 by the Biogeography Branch of NOAA's National Centers for Coastal Ocean Science (Battista and Stecher 2006). To characterize the topography of different depth zones and identify consistent breaks in slope, a depth grid with 3-meter resolution was used to create a raster of slope values using the Spatial Analyst extension in Arcmap 9.1 software. Sections of interest corresponding to the study sites were extracted from the full dataset using the Clip routine. The mean slope was calculated for each one-meter depth interval from 20 to 200 m using the Zonal Statistics Tool. From this data set, average profiles covering the entire study area as well as smaller 300–500 meter sections representative of different regions of the slope were generated. This dataset was used to identify both lateral and vertical (i.e., depth) trends.

Multibeam data were also used to identify sites for more detailed study by ROV and divers. A Seabotix LBV 200 ROV was used to conduct vertical profiles of the slope and qualitatively assess geomorphology and benthic macrofauna. Typical ROV dive profiles extended from the shelf edge down the slope to depths of ~90–100 m, although several dives reached depths in excess of 130 m.

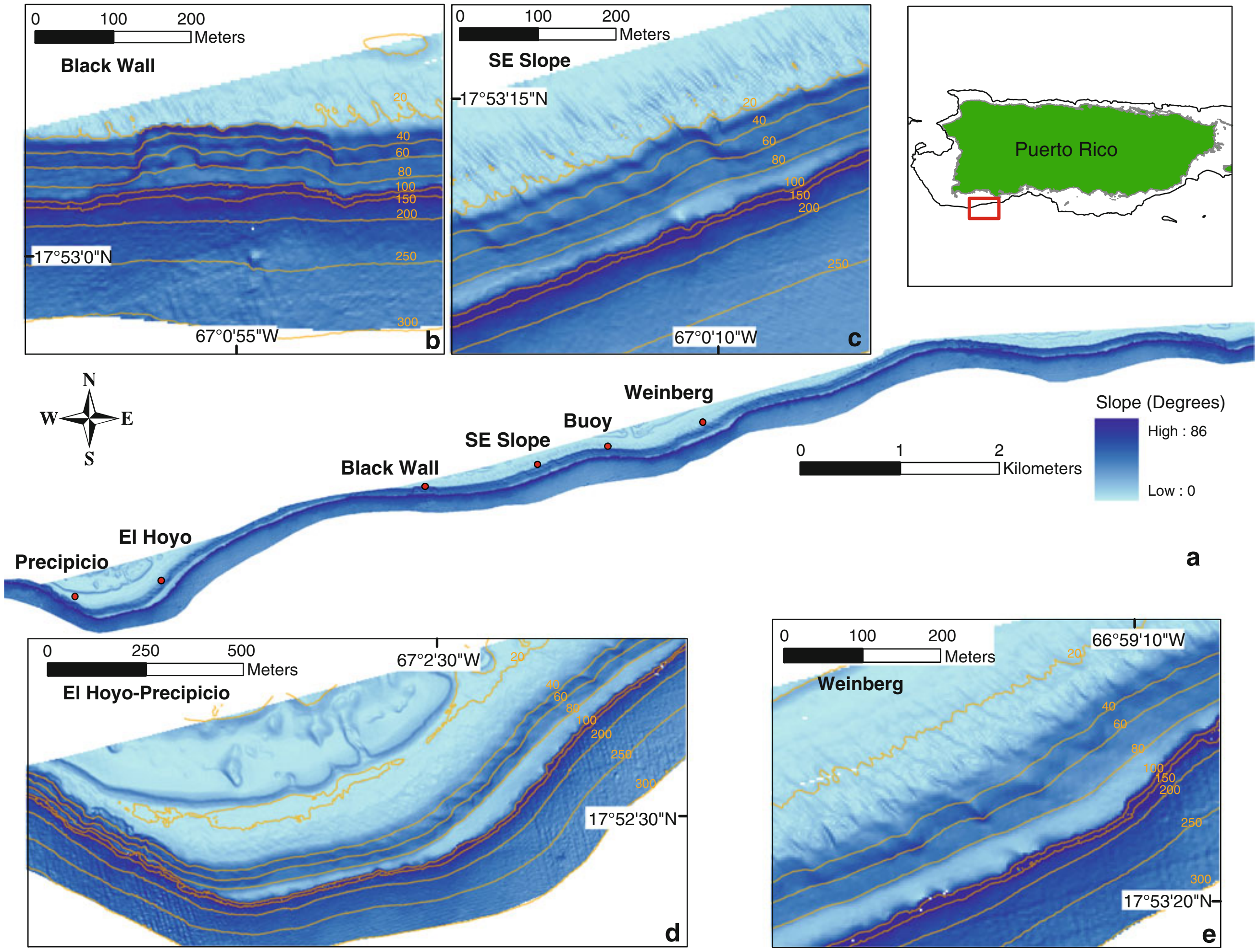

Fig. 1 Multibeam bathymetry of study area. **a** Entire study area. **b** Black Wall. **c** SE Slope. **d** El Hoyo-Precipicio. **e** Weinberg

Continuous video footage was captured on each dive and stored on tapes as well as digitized for later computer evaluation. The ROV was especially important in reaching depths beyond current diving capabilities. A key component of this research was the use of technical, mixed-gas rebreather diving techniques that allowed for in situ surveying of selected sites. Divers were able to survey sites at depths of up to ~80 m, and we expect to extend this range for future studies. Divers made detailed observations of geomorphology and benthic macrofauna as well as careful and targeted collection of hard substrates, sediment and macrofauna, primarily corals and algae, for more detailed study and positive identification in the laboratory. Divers also conducted continuous high-resolution benthic phototransects ~10 m long by 40 cm wide. A total of 17 transects were conducted at three depths at 8 different sites as follows, ~47 m (8 sites), ~59 m (5 sites), ~70 m (4 sites). Individual photographs from the transects, each photo covering an area of ~40 by 60 cm, were analyzed using CPCe point-counting software to determine relative abundances of major groups of benthos and substrate types (Kohler and Gill 2006). Transects were purposely focused on topographic highs where there was a higher abundance and diversity of live coral and benthic cover.

Results

Geomorphology

Geomorphic zones

Geomorphology of the upper slopes of reef-rimmed margins in the Caribbean has been described in locales such as Jamaica (Goreau and Land 1974; Moore et al. 1976), Belize (James and Ginsburg 1979) and the Bahamas (Ginsburg et al. 1991). There are striking similarities in the geomorphology of these areas and the current study area of southwest Puerto Rico. However, previous workers in these different locales have used slightly different terminology to

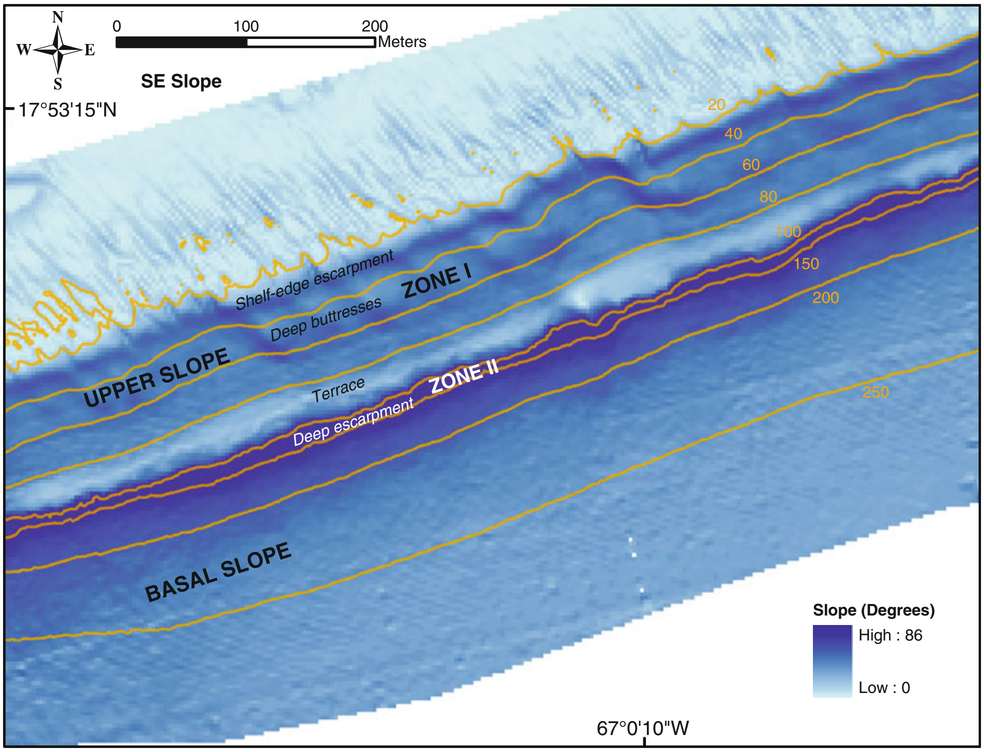

Fig. 2 Multibeam bathymetry of SE Slope showing positions of geomorphic zones and geomorphic features of the upper slope. The upper slope is defined as the region from the shelf break at ~20 m water depth down to a depth of ~160 m where the basal slope begins. The upper slope is divided into two zones, Zone I from 20 to 90 m water depth, and Zone II from 90 to 160 m water depth. Positions of geomorphic features (*italics*) are shown, including the shelf-edge escarpment at ~20–35 m water depth, deep buttresses (~45–65 m water depth), terrace (~80–90 m water depth) and deep escarpment (~90–160 m water depth)

describe similar geomorphic features and patterns of upper slopes resulting in some confusion in the application of these terms (see discussion in Locker et al. 2010). To avoid confusion and possible misappropriate application of pre-existing classification schemes, a more generic approach has been adopted here. The upper insular slope (~20–160 m water depth) of southwest Puerto Rico is divided into two geomorphic zones on the basis of a prominent and consistent break in slope gradient at a water depth of ~90 m. Moving down the slope from the shelf break, typically at a water depth of ~20 m, these are Zone I, ~20–90 m water depth and Zone II, ~90–160 m water depth (Figs. 2 and 3). Within the study area, the gradient of Zone I ranges from ~25° to 45° with an average of 34°, while Zone II has a more uniform and much steeper gradient of ~70°. Smaller-scale geomorphic features found within Zone I include the shelf-edge escarpment (~20–35 m water depth), deep buttresses (~45–65 m water depth) and a prominent terrace at ~80–90 m water depth. Zone II consists of a steep wall (deep escarpment) that drops precipitously from ~90 down to 160 m. The basal slope starts at the base of Zone II (~160 m) where there is a pronounced change in the geomorphic character of the slope.

Zone I: lateral geomorphic trends

Examination of the full ~12-km stretch of the study area reveals a few consistent geomorphic trends related to the direction that the shelf margin and uppermost slope are facing. Southeast-facing slopes have an overall gentler gradient with widely spaced, large-amplitude spur and groove features and a wider, more pronounced terrace at ~80 m (Figs. 1 and 4). The average gradient of Zone I (20–90 m) on southeast slopes is ~29°. In addition, due to the wider spacing of spurs and buttresses, southeast slopes typically display lower topographic relief. In contrast, southwest-facing slopes are consistently steeper (average Zone I gradient of ~44°) with more closely spaced, lower-amplitude spur and groove features. The shelf-edge along these steeper slopes consists of an irregular coral ridge that is intermittently cut by steep narrow grooves. The terrace along southwest slopes, if present, is much narrower and somewhat steeper. Topography on southwest slopes is typically more heterogeneous than on southeast slopes. At several sites along steep southwest slopes, the general geomorphic trend of the shelf edge and slope are interrupted by near-vertical landslide scars several hundred meters across (Fig. 1b). Topography of these scars is steeper and more irregular than

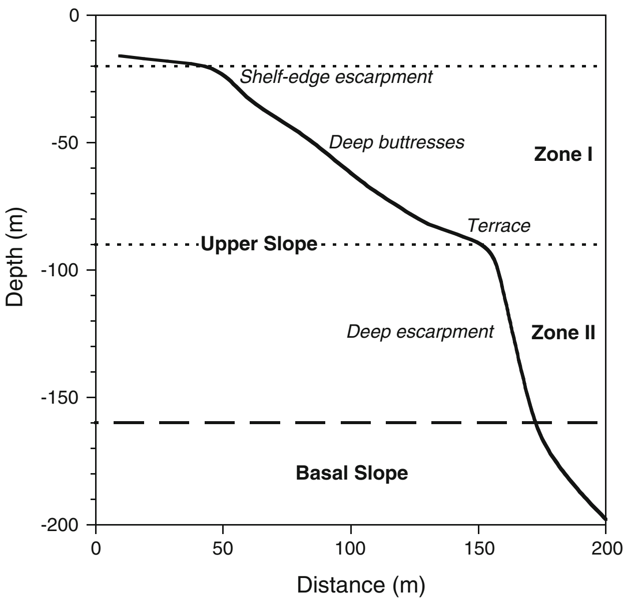

Fig. 3 Average profile of SE Slope shown in Fig. 2 (*black line*). The upper slope is defined as the region from the shelf break at ∼20 m water depth down to a depth of ∼160 m (*heavy dashed line*) where the basal slope begins. The upper slope is divided into two zones, Zone I from 20 to 90 m water depth (*light dashed line*) and Zone II from 90 to 160 m water depth. Positions of geomorphic features (*italics*) are shown, including the shelf-edge escarpment at ∼20–35 m water depth, deep buttresses (∼45–65 m water depth), terrace (∼80–90 m water depth) and deep escarpment (∼90–160 m water depth)

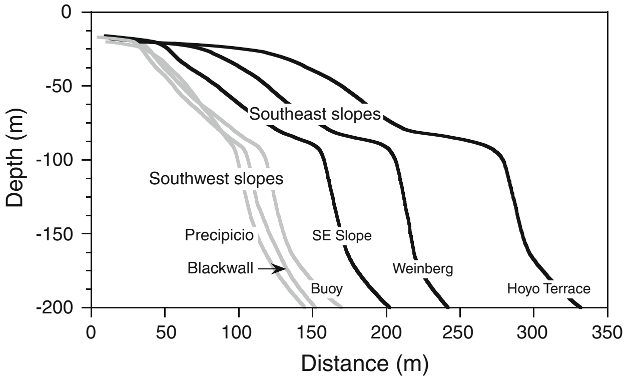

Fig. 4 Average profiles of southeast-facing slopes (*black lines*) and southwest-facing slopes (*gray lines*). Site locations are shown in Fig. 1

other regions due to fissures and slumped blocks. However, the scars still display breaks in slope at depths consistent with other regions in the study area. These lateral trends are evident only in Zone I. Zone II is consistently steep (∼70°) everywhere, with no systematic differences between southeast versus southwest exposures.

Zone I: geomorphic features

Shelf-edge escarpment The shelf-edge escarpment extends from the shelf break at a depth of ∼20 m down to depths of ∼35 m where there is generally a subtle break and decrease in slope gradient. The escarpment is most pronounced and steepest, along southwest slopes where it occurs as a near vertical wall (gradient $\geq 40^\circ$) cut by steep, narrow grooves (e.g., Black Wall and Precipicio, Figs. 1b, d and 5a). Along southeast slopes, the escarpment is not as pronounced (e.g., Weinberg and El Hoyo, Fig. 1d and e). Rather, in these regions there is a gradational increase in gradient moving from the shelf to upper slope. The shelf-edge escarpment is a zone of prolific coral growth that is concentrated on spurs and steep walls. Shelf-edge environments can have some of the highest coral cover found in Puerto Rico and Holocene accretion in these settings often exceeds that of emergent reefs further landward on the shelf (Hubbard et al. 1997, 2008). Skeletal sediment, produced by physical and biological erosion of the surrounding reef, gets funneled into intervening grooves and steep cuts where much of it eventually gets transported down the slope, primarily during storms and large swell events (Hubbard et al. 1990; Hubbard 1992). This downslope sediment transport can exert a fundamental control on the occurrence and distribution of MCEs further down the slope.

Deep buttresses At depths of ∼40–45 m, the slope gradient typically increases again and topography becomes more irregular with prominent buttresses (Fig. 2). Buttresses are large, topographically high features, elongated perpendicular to the shelf edge, with steep seaward fronts that commonly exhibit notches and caves (Fig. 5b). They slope seaward from ∼40 m down to ∼45–50 m where there is a sharp break and a relatively steep wall that drops to ∼60–65 m. On southeast slopes, buttresses are more widely spaced and separated by open, low-relief slopes with lower coral cover and higher amounts of unconsolidated sand. The substrate here consists of a sparsely colonized, well-consolidated hardground that in many cases is covered by a broad, thin sheet of unconsolidated sand. On steeper southwest slopes, buttresses are closer together and separated by narrow, steep-sided sand-floored chutes. Similar buttress features have been described for corresponding depth zones in Jamaica (Goreau and Land 1974) and Belize (James and Ginsburg 1979). The deep buttresses are similar to shallower shelf-edge spur and groove features in both orientation and occurrence. However, buttresses appear to be a separate set of geomorphic features and not necessarily connected to shelf-edge spur and groove.

Coral, predominantly platy corals such as *Agaricia* spp., and other live benthic cover, e.g., algae, sponges, etc., is concentrated on spurs where coral cover can rival that of shallower reefs. The upward and outward accretion of overlapping platy corals gives the spurs a shingled

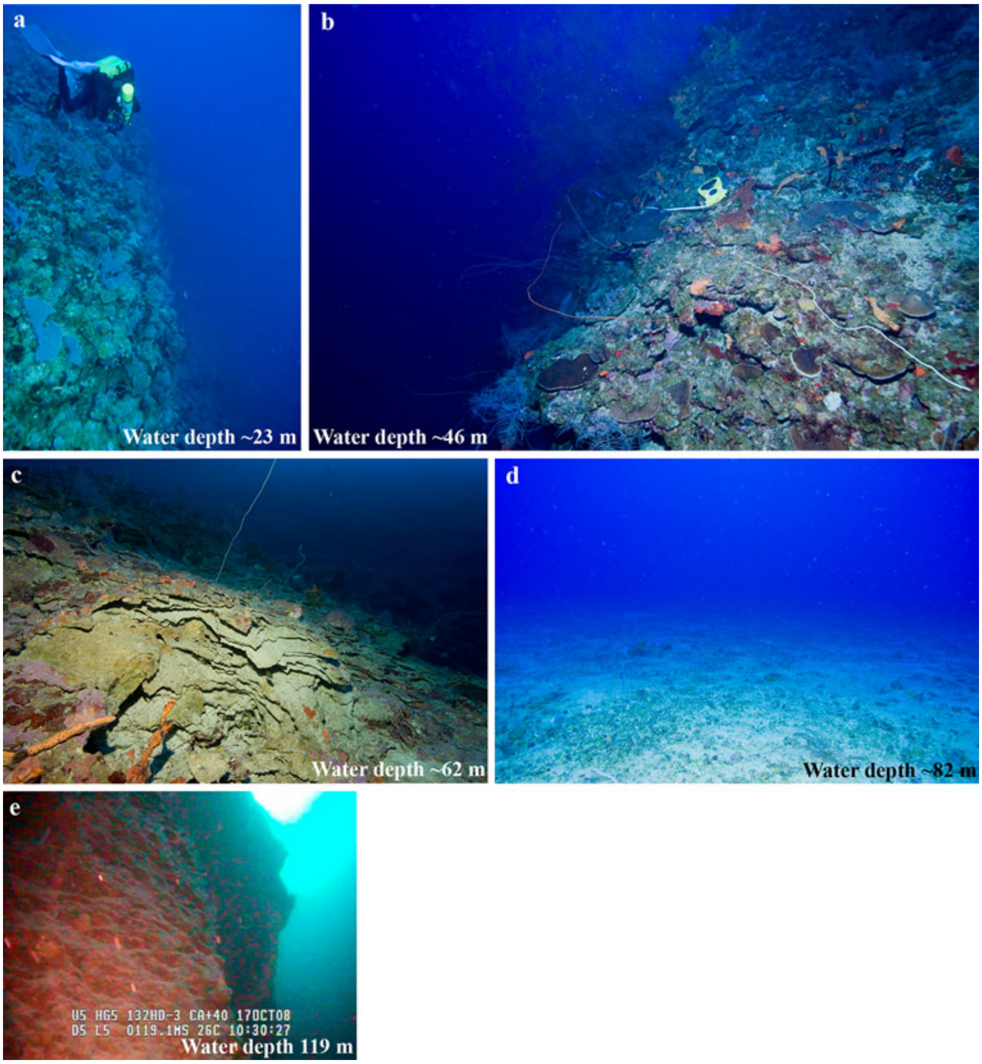

Fig. 5 Geomorphic features of the upper slope. **a** Shelf-edge escarpment at Black wall, a southwest-facing slope. Mass wasting has steepened the escarpment here (diver at ~23 m water depth). **b** Deep buttress at Black Wall. Transect line at ~46 m water depth. **c** Close-up of deep buttress showing shingled structure resulting from vertical accretion of platy corals, primarily *Agaricia* spp., water depth ~62 m. **d** The terrace at El Hoyo, water depth ~82 m. **e** The deep escarpment, water depth 119 m (ROV video capture)

appearance (Fig. 5c). The topographically high spurs provide suitable substrates for corals and other sessile organisms above downslope sediment transport that is funneled into intervening grooves. Additionally, their steep sides and the shingled, platy coral growth allows for easy shedding of any accumulated sediments. Thus, the deep buttresses are prime habitats for mesophotic coral ecosystems.

Terrace The most prominent feature of the upper slope is a pronounced terrace that occurs at a depth of ~80 m (Figs. 1, 2, 3 and 5d). The terrace is widest and most pronounced along southeast slopes where it can be over 50 m wide (Fig. 4). Along these slopes, it dips gently seaward at an average gradient of ~17° from depths of ~80 m down to ~90 m water depth where there is another precipitous break in slope and the deep escarpment of Zone II begins. In general, the terrace is low-relief with a covering of sand and fairly barren compared to shallower regions of the slope described previously. Sporadic patches of sponges and octocorals occur where rocky outcroppings and hard substrates are available. Where downslope sediment transport from above is reduced, the terrace is more of a hardground and there is a corresponding increase in live benthic cover. Corals are rare or absent on the terrace and have only been noted along its seaward margin, particularly in regions where the transition between the terrace and wall is not as abrupt.

Zone II: geomorphic features

Deep escarpment At a depth of ~90 m (i.e., the seaward margin of the terrace), there is a consistent and precipitous break in slope where the terrace gives way to the deep escarpment (Figs. 2 and 3). This also represents the transition from Zone I to Zone II of the upper slope. The deep escarpment of Zone II is a near-vertical to overhanging wall that drops from ~90 m down to ~160 m water depth. However, for this project, only the upper portions of the escarpment down to ~130 m have been viewed by ROV. Similar walls have been described in Jamaica (Goreau and Land 1974; Moore et al. 1976), Belize (James and Ginsburg 1979) and the Bahamas (Ginsburg et al. 1991). The deep escarpment often consists of a stacked series of irregular and discontinuous ledges of various sizes that give it a layered appearance (Fig. 5e). The stacked ledges are interrupted by featureless cliffs or caves and vertical fissures that run down the escarpment perpendicular to the strike of the ledges. Ledges and other gently sloping surfaces are typically covered by a layer of fine, light-colored sediment. Live benthic cover is patchy on the deep escarpment. Corals are rare with only a few occurrences noted, primarily around the slope break at 90 m. Scattered octocorals and antipitharians occur along vertical portions of the escarpment. Close examination of the deep escarpment shows that it is often covered by a veneer of crustose coralline algae and sponges. At a depth of ~160 m, the deep escarpment gives way to an open, low-relief slope, i.e., the basal slope (Figs. 2 and 3). While not directly observed, multibeam bathymetry suggests that this region is a reef-talus slope similar to those described in Jamaica (Goreau and Land 1974; Moore et al. 1976), Belize (James and Ginsburg 1979) and the Bahamas (Ginsburg et al. 1991).

Benthic cover

Benthic cover was divided into eight major categories, which are coral, sponges, non-calcareous macroalgae, *Halimeda*, coralline algae, Peyssonneliaceae, uncolonized sand and a final category that covers points not identifiable in the photographs. For this study, coral refers to scleractinian corals. Non-calcareous macroalgae refers to forms such as *Dictyota*, *Wrangelia* and *Lobophora*. The other algal categories are calcareous forms and important as encrusters and secondary frame-builders, such as coralline algae and members of the Peyssonneliaceae, or as sediment contributors, such as *Halimeda*. As this study was focused on mesophotic coral ecosystems, transects were purposely placed in areas of relatively higher coral cover and overall benthic diversity. Thus, these results should be viewed as a preliminary assessment of these ecosystems and not an overall quantification of benthic cover over the depth range studied. Combining results from the three depths studied, i.e., ~47, 59 and 70 m, shows that non-calcareous macroalgae is the dominant benthic cover with a relative abundance of over 30%, followed by sponges (~15%), corals (~13%) and coralline algae (~12%) (Table 1). Peyssonnelioids and *Halimeda* account for less than 10% of benthic cover. Taken together, all algal categories, i.e., macroalgae, *Halimeda*, coralline algae and Peyssonneliaceae, account for over 50% of benthic cover. Uncolonized sand accounts for ~18% of the area studied. Non-calcareous macroalgae consists predominantly of *Lobophora variegata* and several species of *Dictyota* and *Wrangelia*. In general, algal cover was high wherever suitable hard or semi-consolidated substrate was available. Corals consist predominantly of species of *Agaricia* and *Madracis*. Corals, coralline algae and *Halimeda* increase in relative abundance with depth, while non-calcareous macroalgae and peyssonnelioids decrease in abundance with depth.

Coral diversity and relative abundances

A total of 17 species of scleractinian coral belonging to 8 genera have been identified from photo transects, diver observations and ROV video from 8 sites between 50 and 90 m water depth (Tables 2 and 3). Their distribution and relative abundances were highly variable along the depth gradient and across localities at the same depth interval. Corals are concentrated on topographic highs such as the deep buttresses and more widely dispersed on vertical walls. Intervening areas of low relief and, presumably, higher downslope sediment transport, have lower amounts of live cover that is typically dominated by sponges, macroalgae and coralline algae. Percentages reported here (Tables 2 and 3) refer to the relative abundance of coral genera or species within the coral community.

Combining and averaging results from the three depths studied shows that the family Agariciidae represented by *Agaricia* and *Undaria,* is the dominant group in terms of abundance and cover followed by *Madracis, Montastraea* and *Stephanocoenia* (Table 2). *Undaria* is recognized as a coral genus within the family Agariciidae following the

Table 1 Percent benthic cover in the mesophotic zone on the upper insular slope of southwest Puerto Rico based on photo-quadrat transects at 47, 59 and 70 m

Benthic cover category	Transect depth			Average
	47 m	59 m	70 m	
Coral	5.1	7.4	27.7	13.4
Sponges	16.2	16.9	13.4	15.5
Non-calcareous macroalgae	45.2	42.1	8.0	31.8
Halimeda	0.2	0.9	5.0	2.0
Coralline algae	5.9	10.4	19.1	11.8
Peyssonneliaceae	9.0	4.9	4.4	6.1
Sand	17.6	15.9	20.9	18.1
Unidentified	0.7	1.6	1.3	1.2

Table 2 Relative abundances (%) of scleractinian genera within the mesophotic coral community on the upper insular slope of southwest Puerto Rico based on photo-quadrat transects at 47, 59 and 70 m. Numbers in parentheses indicate percent total coral cover (see Table 1)

Scleractinian genera	Transect depth			Average (13.4)
	47 m (5.1)	59 m (7.4)	70 m (27.7)	
Agaricia	45.5	49.2	75.0	56.6
Undaria	14.9	13.1	0.0	9.3
Montastraea	9.9	5.0	1.2	5.4
Stephanocoenia	4.0	3.5	4.8	4.1
Madracis	21.8	28.6	19.0	23.2
Porites	–	0.5	–	0.2
Siderastrea	3.0	–	–	–
Scolymia	1.0	–	–	0.3

taxonomy of Stemann (1991) that divides *Agaricia* into two separate genera, *Agaricia* and *Undaria*. Relative abundance of *Agaricia* colonies increased with depth, from 45% at 47 m to 75% at 70 m (Table 2), but the specific abundances varied with *A. lamarcki* dominating at 47 m (~24%), while *A. undata* (a new depth record for Puerto Rico) was the dominant species (~68%) in deeper habitats (Table 3), sometimes forming large colonies on top of spur formations (Fig. 6). Although *Agaricia* becomes the dominant coral by depths of ~50 m, these exceptionally large colonies were not noted until depths of ~60–70 m. *A. fragilis* was observed only in the upper depth intervals (47 and 59 m), while *A. grahamae* was common at all three depths. Both of these species showed their highest abundance at the intermediate depth (59 m). *Undaria* was observed only at the two shallower transect depths at 47 and 59 m (Table 2). *Undaria humilis* was observed at 59 m, probably the deepest report for this species, and *U. agaricites* was found only at the 59-m transect depth (Table 3).

The genus *Madracis* was the second most abundant group with *Madracis pharensis* (both *forma luciphylla* and *forma luciphogous*) showing higher abundances at the intermediate depth (59 m) (Tables 2 and 3). The azooxanthellate form (*M. pharensis luciphogous*) was significantly more abundant and had a deeper depth range, being found at all three transect depths. Two other species in this genus were observed in very low abundances, *M. decactis* in one of the photo-quadrats and a large colony of *M. formosa* outside the quadrats (Table 3). *Stephanocoenia intersepta* had low but consistent abundances along the depth gradient. A few colonies of *Montastraea franksi* were observed at 47 m. *M. cavernosa* was more abundant in shallower habitats, but has been observed down to 90 m. The common reef building *Siderastrea siderea* was found only down to 47 m, and a single colony and two polyps of *Mycetophyllia ressi* and *Scolymia cubensis*, respectively, were observed (Table 3).

Discussion

Geomorphology and mesophotic coral ecosystems

Wave energy is known to exert an important control on reef morphology and ecology. Ecological zonation along reef fronts in the Caribbean has been correlated to wave exposure (Adey and Burke 1977; Geister 1977; Hubbard et al. 2008). Topographic profiles of reefs, formation of geomorphic structures such as spur and groove topography and sediment transport in reef systems are all closely linked to wave characteristics (Shinn 1963; Roberts et al. 1977; Sneh and Friedman 1980; Hubbard et al. 1981; Blanchon and Jones 1997; Storlazzi et al. 2003). Along the southwest coast of Puerto Rico, prevailing trade-wind-generated swell approaches from the southeast (cf. Hubbard et al. 2008). Tropical cyclones also typically approach Puerto Rico from the southeast (cf. Hubbard et al. 2008). Thus, along the south coast of Puerto Rico, southeast-facing slopes are more exposed and on average would be expected to experience higher energy conditions than southwest-facing slopes. In the region studied, Zone I (20–90 m water depth) of southeast-facing slopes consistently has a gentler gradient than Zone I of southwest slopes (Fig. 4). In addition, spur and groove topography oriented perpendicular to the shelf margin and parallel to prevailing wave direction (i.e., southeast-northwest) is more pronounced along southeast slopes, with widely spaced, large-amplitude spur and groove features, both at the shelf-edge escarpment and further down the slope at ~45–65 m in the form of deep buttresses (Fig. 1). In contrast, southwest-facing slopes are steeper with less pronounced, more closely spaced, lower-amplitude spur and groove features. This relationship between wave exposure and upper slope morphology is similar to that described for the insular shelf margin of Grand Cayman where exposed margins exhibited large-amplitude spur and groove features, while along leeward margins spur and groove topography was not as evident (Blanchon and Jones 1997). In addition, the seaward front of submerged shelf-edge reefs along exposed windward margins in Grand Cayman had a gentler gradient than those along leeward margins (Blanchon and Jones 1997). Shelf-edge spur and groove topography appear to be maintained and enhanced by high-energy conditions during storms and large-swell events. Strong currents and oscillatory wave flow established at these times are capable of pruning spurs and scouring grooves leading to a wholesale flushing of sand and rubble from the shelf edge down to deeper zones

Table 3 Relative abundances (%) of scleractinian coral species within the mesophotic coral community on the upper insular slope of southwest Puerto Rico based on photo-quadrat transects at 47, 59 and 70 m

Scleractinian species	Transect depth			Average (13.4)
	47 m (5.1)	59 m (7.4)	70 m (27.7)	
Agaricia lamarcki	23.8	9.5	3.4	12.2
A. fragilis	18.8	17.1	–	12.0
A. grahamae?	3.0	20.1	4.5	9.2
A. undata	–	2.5	68.2	23.6
Undaria agaricites	–	5.5	–	1.8
U. humilis	14.9	7.5	–	7.5
Montastraea franksi	4.0	–	–	1.3
M. cavernosa	5.9	5.0	1.1	4.0
Stephanocoenia intersepta	4.0	3.5	4.5	4.0
Madracis pharensis luciphylla	6.9	9.0	3.4	6.5
M. pharensis luciphogous	11.9	19.6	14.8	15.4
M. decactis	3.0	–	–	1.0
M. formosa?	–	X	–	–
Porites astreoides	–	0.5	–	0.2
Siderastrea siderea	3.0	–	–	1.0
Scolymia cubensis	1.0	–	–	0.3
Mycetophyllia reesi	–	X	–	–

Numbers in parentheses indicate percent total coral cover (see Table 1). X = species observed out of the quadrats not included in the quantitative analyses. ? = species needs verification

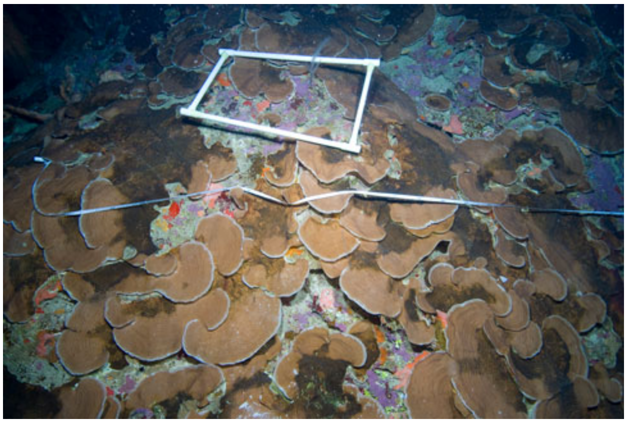

Fig. 6 A large colony of *Agaricia undata* at 76 m water depth. Quadrat size 40 by 60 cm

on the slope (Hubbard et al. 1981; Hubbard 1992; Blanchon and Jones 1997). In addition, course reef detritus supplied to the upper slope by repeated pruning of shelf-edge spurs facilitates progradation (i.e., seaward lateral accretion) of the spurs and a gentler seaward gradient (Blanchon and Jones 1997). Thus, higher wave energy along southeast slopes would be expected to lead to progradation of shelf-edge spurs and increased downslope sediment transport in these regions. In contrast, lower wave energy along southwest slopes results in enhanced vertical accretion of shelf-edge reefs, a steeper seaward front, and reduced downslope sediment transport (cf. Blanchon and Jones 1997).

The gentler gradient of Zone I of southeast slopes is consistent with increased reef progradation and downslope sediment transport along these more exposed margins. The gentler gradient of the shelf-edge escarpment along southeast slopes is likely a result of recent progradation of spurs (cf. Blanchon and Jones 1997). The pronounced deep buttresses and wide terrace on southeast slopes may reflect enhanced reef progradation during preexisting sea-level stands below present. Increased downslope sediment transport on southeast slopes facilitates and maintains an overall gentler gradient. Hubbard (1986) and Hubbard et al. (1986) found that slopes on St. Croix that experienced increased sedimentation had a gentler gradient and reduced live cover consisting of gorgonians, sponges and sediment-tolerant corals. These slopes consisted of cemented hard-grounds with a discontinuous veneer of sandy sediment. This description is similar to the open southeast-facing slopes below the shelf-edge escarpment along the southwest insular margin of Puerto Rico. Prolific coral growth and associated carbonate production at the shelf edge produces copious sediment, some portion of which is transported downslope. On lower-gradient, lower-relief southeast slopes, this sediment has a longer residence time and is spread over a wider area, i.e., the open slopes between widely spaced deep buttresses. In contrast, on steeper southwest-facing slopes, sediment is quickly funneled into steep narrow grooves and transported downslope. It, therefore, has a lower residence time and affects a smaller area.

On insular slopes, MCEs need to be adapted to the persistent downslope transport of sediment. They do so by being concentrated on topographic highs, e.g., spurs, buttresses, etc., elevated above the surrounding seafloor and removed from the influence of prevailing downslope sediment movement. On exposed southeast slopes, topographic highs are fewer and farther between and are separated both laterally and vertically by open low-relief slopes where sediment accumulation and/or transport inhibits coral recruitment and growth. Accordingly, MCEs are also patchy and widely spaced on southeast slopes. On steep, irregular southwest slopes, suitable topographic highs are more abundant and more closely spaced. Downslope sediment transport is restricted to narrow grooves. This results in MCEs being more abundant, extensive and diverse on southwest slopes. At several sites on southwest slopes, prolific coral growth extends uninterrupted from the shelf break down to depths of 80 m or more. Landslide scars along southwest slopes are especially important sites for MCEs due to their exceedingly steep and irregular topography. These relationships reinforce the fundamental control that geomorphology and sediment transport exert on the occurrence and distribution of mesophotic coral ecosystems.

It is important to point out that the relationships just described between slope gradient and MCEs is specific to slope environments where there is an upslope source of sediment and downslope sediment transport exerts a fundamental control on benthic communities. In other settings around Puerto Rico, vibrant MCEs have been described occurring on relatively flat or gently sloping terraces (Garcia-Sais et al. 2005, 2008; Armstrong et al. 2006). These MCEs occur on outer insular shelves south of Vieques and the US Virgin Islands where there are large areas of the shelf at mesophotic depths isolated from any downslope sediment transport. Thus, extensive MCEs are able to thrive in these settings.

Benthic cover

Results on benthic cover presented here are similar to those described by Garcia-Sais et al. (2005, 2007) for reefs at ~30–50 m water depth at Isla Desecheo and Bajo de Sico Seamount, Puerto Rico. They describe a similar dominance of algal cover as well as a dominance of *Agaricia* within the coral community at their deeper sites at ~50 m. Armstrong et al. (2006) recorded higher coral cover (~43%) on deep insular shelf reefs in the US Virgin Islands at depths between 33 and 47 m. However, these reefs were dominated by the *Montastraea annularis* complex and, importantly, located on top of the shelf rather than on the insular slope as are the coral ecosystems being described in this study.

Although fewer transects were completed at the deeper sites and sampling is biased toward sites with relatively high coral cover, comparing results from the three different study depths does suggest some consistent trends that may be born out with additional surveys and sampling (Table 1). A decrease in macroalgae and peyssonnelioids with depth might be expected given decreasing light availability. However, the dramatic drop in macroalgal cover is more likely a result of the few deep transects completed having exceptionally high coral cover. Additional data would undoubtedly smooth these trends. Still, these results indicate that high-density coral communities do occur at these depths along the insular slope. The subtle increase in *Halimeda* and coralline algae probably reflect real trends. The importance of these groups as benthic cover, frame-builders and/or sediment producers has been noted in the deep reef front environments of Belize (James and Ginsburg 1979) and the Bahamas (Ginsburg et al. 1991). With respect to coral depth distributions and relative abundances, the species reported here have been reported from other MCE areas of the wider Caribbean (Goreau and Wells 1967; Goreau and Goreau 1973; Wells 1973; Lang 1974; Reed 1985; Stemann 1991; Garcia-Sais et al. 2005, 2008; Armstrong et al. 2006; Lumsen et al. 2007). Thus far, surveys and observations by divers have been conducted down to depths of ~80 m, while ROV observations extend down to ~130 m water depth. In combination, these observations indicate that in this region MCEs are largely restricted to Zone 1 (20–90 m water depth). Only a few occurrences of corals were noted within Zone II, primarily around the slope break at ~90 m water depth. As research and surveys advance, a clearer picture of the distribution, habitat preferences, abundances and cover of each particular scleractinian taxa will emerge.

Relict features

As early as 1967, Macintyre (1967) proposed that a narrow ridge rising from a water depth of 80 m up to ~70 m on the insular slope off the west coast of Barbados was a relict reef formed during a preexisting sea-level stand below present. Similar submerged ridges and terraces have been identified around the Caribbean including Jamaica, western Guiana and Puerto Rico (see Macintyre et al. 1991; Macintyre 2007). Submerged terraces at these depths have also been noted along the seaward margin of the Great Barrier Reef (Harris and Davies 1989; Beaman et al. 2008). Barbados is one of the few locales where these submerged structures have been cored and their composition and age verified (Fairbanks 1989). Coring and radiometric dating by Fairbanks (1989) and Bard et al. (1990) showed that submerged structures off the south coast of Barbados are relict shallow-water reefs formed during the last deglaciation. Subsequently, reef systems in other locales and tectonic settings, including Tahiti (Bard et al. 1996) and Papua New Guinea (Chappell and Polach 1991; Cutler et al. 2003), have been cored and dated and have provided crucial information on the timing and nature of sea-level rise during the last deglaciation. In particular, these records reveal that sea-level rise during the last deglaciation was episodic and characterized by at least two periods of rapid sea-level rise associated with global meltwater pulses at ~14 and 11.3 ka referred to as meltwater pulses 1A and 1B, respectively (Fairbanks 1989; Bard et al. 1990, 1996). As indicated in Fig. 7, meltwater pulse 1A is the more clearly established of the two in the geologic record and caused up to 20 m of sea-level rise in less than 500 years (Fairbanks 1989; Bard et al. 1990, 1996; Webster et al. 2004b). Meltwater pulse 1B appears to have been smaller and its occurrence is still under debate (Bard et al. 1996). Based on these reef-accretion records, it is possible to propose an age for the submerged features found on the insular slope of southwest Puerto Rico (Fig. 7). Although Puerto Rico is in a tectonically active setting, proposed uplift rates for the island are relatively moderate, on the order of 0.03–0.05 m/ky (Taggart 1992; Muhs et al. 2005). Thus, over the timeframe of the last deglaciation, the island can be considered to be relatively stable.

The most prominent feature on the upper insular slope off southwest Puerto Rico is a pronounced terrace at a depth of ~80 m (Figs. 1 and 2). Seiglie (1971) also noted a “Pleistocene reef at 80–85 meters of depth” off the west of Puerto Rico. Off southwest Puerto Rico, the terrace is widest on southeast-facing slopes. Spur and groove topography is also most pronounced on southeast slopes, which implies a link between processes responsible for the formation of these different geomorphic structures. The 80-m terrace may be a constructional feature, e.g., a relict reef, or an erosional feature, e.g., a wave-cut platform. Either feature implies a period of stable or moderately rising sea level allowing for formation of the reef or wave-cut platform, followed by a period of relatively rapid sea-level rise drowning the feature and leaving it behind as a relict. Based on the age and depth of deglacial shallow-water reefs and shoreline facies from other locales, it is proposed that the 80-m terrace in Puerto Rico

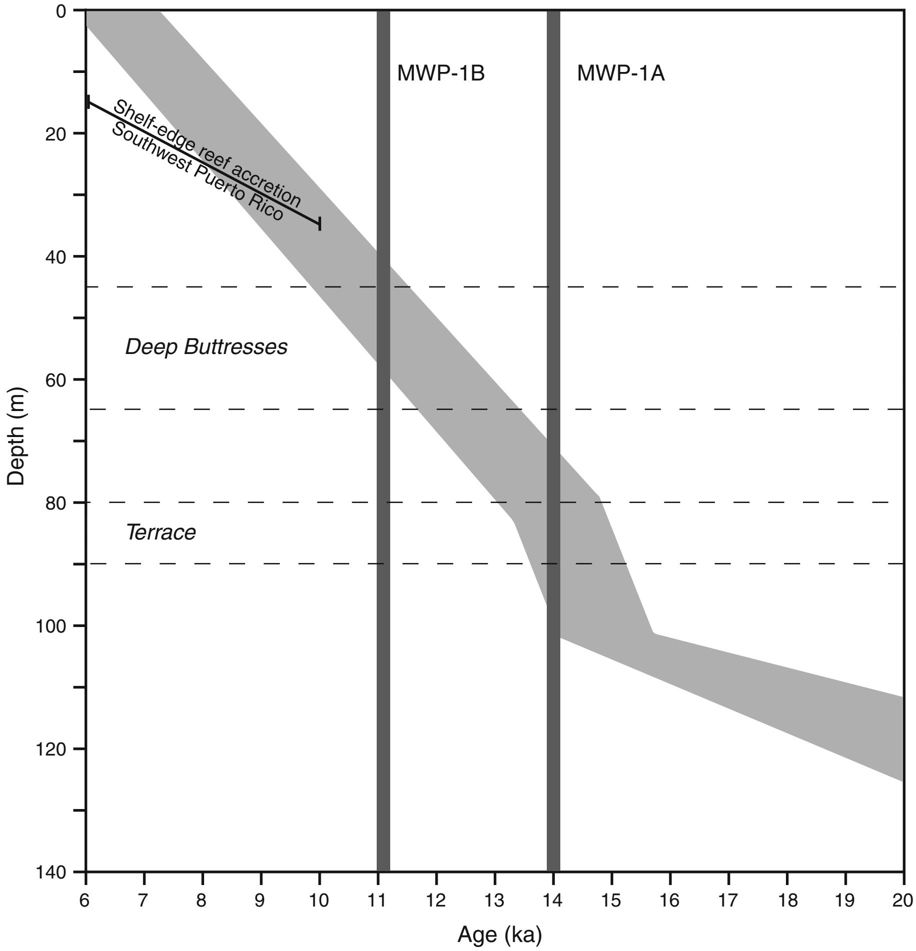

Fig. 7 Age and depth of shallow-water corals based on data from Barbados (Fairbanks 1989; Bard et al. 1990), Tahiti (Bard et al. 1996) and Papua New Guinea (Chappell and Polach 1991; Cutler et al. 2003) and shoreline facies from the Sunda Shelf (Hanebuth et al. 2000). Timing of meltwater pulses 1A and 1B (Fairbanks 1989; Bard et al. 1990; Bard et al. 1996) indicated by *vertical dark gray bars*. Timing and depth of shelf-edge reef accretion in southwest Puerto Rico indicated by *black line* in *upper left corner* (Hubbard et al. 1997; Hubbard et al. 2008). Depth of prominent geomorphic structures on the insular slope of southwest Puerto Rico, i.e., deep buttresses and terrace, indicated by *horizontal dashed lines* (after Beaman et al. 2008)

was formed during the last deglaciation ~14–15 ka and then drowned during a period of rapid sea-level rise at ~14 ka, meltwater pulse 1A (Fig. 7).

Moving up the slope, the next prominent features encountered are deep buttresses at depths of ~45–65 m (Figs. 1 and 2). Although the deep buttresses are similar to shelf-edge spur and groove in occurrence and orientation, the buttresses appear separate and disconnected from shelf-edge spur and groove, i.e., they are not simply extensions of shelf-edge features. As spur and groove formation is closely linked to wave processes, deeper occurrences of these features at depths beyond 20–30 m are generally thought of as relict features from lower sea-level stands (Rooney et al. 2008). Similar buttress features at depths of ~40–65 m have been reported at several locales including Jamaica (Goreau and Land 1974), Belize (James and Ginsburg 1979), and the Northwest Hawaiian Islands (Rooney et al. 2008). An extensive line of drowned shelf-edge reefs at depths of 40–70 m have also been documented on the seaward margin of the Great Barrier Reef (Beaman et al. 2008). On the insular slope of Oahu, Hawaii, a complex of erosional notches are carved into a paleoreef at depths ranging from 49 to 67 m (Fletcher and Sherman 1995). Once again comparing the depth of the deep buttresses in Puerto Rico with records from other locales, it is proposed that the buttresses are relict features originally formed between ~11.5 and 13.5 ka and then drowned during a period of rapid sea-level rise at ~11.3 ka, meltwater pulse 1B (Fig. 7). The deep buttresses are especially important to MCEs as the topographically high features provide suitable hard substrates above downslope sediment transport for the development of MCEs. It is likely that the MCEs described here are relatively recent thin veneers over preexisting shallow-water formations. Undoubtedly, Holocene portions of the terrace and deep buttresses are built upon similar Pleistocene foundations formed by repeated cycles of submarine deposition and subaerial erosion as a result of glacio-eustatic sea-level fluctuations during the Quaternary.

Coring studies by (Hubbard et al. 1997, 2008) show that Holocene shelf-edge reef accretion in southwest Puerto Rico began on Pleistocene foundations approximately 30–35 m below present sea level at ~10 ka (Fig. 7). These reefs were composed predominantly of *Acropora palmata* and actively accreted upward 15–20 m until ~6 ka when vigorous vertical accretion quite inexplicably ceased at the shelf edge. Modern coral cover in these areas, consisting primarily of deeper water massive species, is a relatively thin veneer over the relict *Acropora* reefs. Concurrently, inner and mid-shelf reefs began accreting ~8 ka and continued to build vertically throughout the Holocene up to modern sea level. If the proposed scenario for formation of the 80-m terrace and deep buttresses are correct, the insular slope off southwest Puerto Rico represents an important and unique record of deglacial sea-level rise and reef accretion. A coring study of the relict features on the slope could confirm the proposed scenario and, in conjunction with the previous work by Hubbard et al., generate an unparalleled record documenting deglacial backstepping of reefs up the slope and across the shelf and the response of reef ecosystems to changing environmental conditions.

Acknowledgments Milton Carlo, University of Puerto Rico-Mayagüez (UPRM), Department of Marine Sciences Diving Safety Officer was an integral component of the diving team and also provided extensive logistical support throughout field operations. Doug Kessling, Thor Dunmire and Scott Fowler, National Oceanic and Atmospheric Administration (NOAA) Undersea Research Center, University of North Carolina Wilmington and Tony Cerazo, Puerto Rico Technical Diving Center, assisted with both diver training and field operations support. This work was supported by funding from NOAA's Center for Sponsored Coastal Ocean Research (Award No. NA06NOS4780190) to the Caribbean Coral Reef Insitute of UPRM.

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