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REVIEW

Geomorphology of mesophotic coral ecosystems: current perspectives on morphology, distribution, and mapping strategies

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Abstract This paper presents a general review of the distribution of mesophotic coral ecosystems (MCEs) in relationship to geomorphology in US waters. It was specifically concerned with the depth range of 30–100 m, where more than 186,000 km^2 of potential seafloor area was identified within the US Gulf of Mexico/Florida, Caribbean, and main Hawaiian Islands. The geomorphology of MCEs was largely inherited from a variety of pre-existing structures of highly diverse origins, which, in combination with environmental stress and physical controls, restrict the distribution of MCEs. Sea-level history, along with depositional and erosional processes, played an integral role in formation of MCE settings. However, mapping the distribution of both potential MCE topography/substrate and existing MCE habitat is only beginning. Mapping techniques pertinent to understanding morphology and MCE distributions are discussed throughout this paper. Future investigations need to consider more cost-effective and remote methods (such as autonomous underwater vehicles (AUVs) and acoustics) in order to assess the distribution and extent of MCE habitat. Some understanding of the history of known MCEs through coring studies would help understand their initiation and response to environmental change over time, essential for assessing how they may be impacted by future environmental change.

Keywords Mesophotic · Coral · Geomorphology · US Waters

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Introduction

This paper reviews the distribution and occurrence of mesophotic coral ecosystems MCEs (Puglise et al. 2009; Hinderstein et al. 2010) and the geological processes that control their distribution and characteristics. The ultimate objective is to provide a background for assessing needs for future research. It begins with an assessment of the potential spatial extent of MCEs on continental and insular shelves for water depths between 30 and 100 m. It reviews examples of specific geomorphology for areas of the US Caribbean, Gulf of Mexico (GOM), and tropical Pacific, which provides a context to assess current ideas of MCE occurrence and potential distribution. As mapping is an essential component for MCE investigations, a section is included that reviews approaches for mapping technologies related to MCEs. The paper concludes by considering critical needs for future research related to the geomorphology of MCEs. Several additional science papers were prepared for inclusion in this special publication that report on the geomorphology and related characteristics of MCEs (Bare et al. 2010; Rooney et al. 2010; Sherman et al. 2010).

Potential MCE distribution in Northern Gulf of Mexico, Florida, the US Caribbean, and the Main Eight Hawaiian Islands

While previous GIS-based analyses have been conducted to estimate potential shallow-water ecosystems of the United States (Rohmann et al. 2005), these efforts were limited in their ability to characterize deeper coral ecosystems, explicitly mesophotic coral ecosystems. The distribution of MCEs is determined by the suitable combination of a number of factors including geomorphology, sedimentation, light availability, and temperature gradients. Consistent and comprehensive synoptic information on the distribution of these variables at appropriate spatial scales is presently unavailable, preventing statistically robust means of predicting mesophotic distribution. In lieu of this capability, a bathymetric depth range of 30–100 m was used as a surrogate for predicting the potential for occurrence of MCEs for three regions in the US (Caribbean, Gulf of Mexico, and main Hawaiian Islands). These depth limits were determined to represent a minimum range through consensus by participants at the NOAA Mesophotic Coral Ecosystem Workshop held in Jupiter, FL in July 2008 (see Hinderstein et al. 2010). While individual MCEs have been well documented off the coasts of Puerto Rico and the US Virgin Islands, little is known about the broad-scale geographic distribution of these vital marine resources. Mapping the location and size of potential MCE areas will assist scientists and resource managers to better target additional research, mapping, and characterization efforts of MCEs in the coastal waters of the US.

Georeferenced images of the bathymetry of Florida (FL), northern Gulf of Mexico (NGM), the US Caribbean (USC), and the main eight Hawaiian Islands (MHI) were compiled to identify locations that were potentially suitable for MCEs, based on depth (30–100 m). These datasets were acquired as US Coastal Relief Model ASCII Grids freely available from NOAA's NGDC website (Divins and Metzger 2008). Sources for these bathymetric surfaces include the US National Ocean Service Hydrographic Database, the US Geological Survey (USGS), Monterey Bay Aquarium Research Institute (MBARI), US Army Corps of Engineers LIDAR (SHOALS), and various other academic institutions. Volumes 3 through 5 (Divins and Metzger 2008) also use bathymetric contours from the International Bathymetric Chart of the Caribbean Sea and the Gulf of Mexico project as input to the gridding process. Topographic data are from the USGS 3-arc-second DEMs and Shuttle Radar Topography data (SRTM).

The shoreline and the 30, 100, and 1,000 m isobaths were extracted from the above bathymetric dataset using the *Reclassify* function in ArcGIS 9.2 Spatial Analyst Extension. Specifically, the raster was reclassified as follows:

$>$0 m = No Data (land)
0 to $-$29.9 m = 30 m isobath
$-$30 to $-$99.9 m = 100 m isobath
$-$100 to $-$999.9 m = 1,000 m isobath
$<-$1,000 m = No Data

The rasters were projected into the World Sinusoidal (equal area) coordinate system to ensure the integrity of the area calculations. They were also projected into the World Equidistant Cylindrical (equal distance) coordinate system to ensure the integrity of the distance calculations. The area between each island in the US Caribbean and main Eight Hawaiian Islands was divided based on Euclidean distance in order to understand how potential MCE habitat varied by island. This distance was calculated using ArcGIS's SA Euclidean Allocation function, and the resulting surfaces were used to define the area on the seafloor closest to each island.

Analysis of the potential MCE areas indicate that the northern Gulf of Mexico/Florida (178,867 km^2) region has an order of magnitude greater potential area than either the US Caribbean (3,892 km^2) or main Hawaiian Islands (3,299 km^2) (Figs. 1, 2, 3). Although the spatial extend of mesophotic depths is large in the Gulf of Mexico, the potential for MCEs may be somewhat reduced by turbid water and circulation patterns in the central Gulf (i.e., Mississippi River input). Nonetheless, the broad gently sloping shelf located within the northern Gulf of Mexico and west side of the Florida Platform contributes to high potential MCE area, in contrast to comparatively steep bathymetric slopes in the US Caribbean and main Hawaiian Islands. The notable exceptions to this trend include large expanses of potential MCEs due north of Culebra, Puerto Rico to St. John, USVI; due east of Vieques, Puerto Rico to St. John, USVI; Penguin Bank extending southwesterly from Molokai, HI, and the pass between Lanai and Maui, HI. While in situ studies on mesophotic distribution are limited, the spatial predictions presented here correlate well with documented mesophotic coral communities at the Flower Garden National Marine Sanctuary off the coast of Texas, Pulley Ridge due east of the Florida Keys, and Red Hind and Grammanik Banks located south of St. Thomas, USVI.

Several investigations into the Caribbean have demonstrated that coral communities located further from land may be insulated from the deleterious anthropogenic and oceanographic stressors experienced by most shallow reef systems (Armstrong et al. 2006; Menza et al. 2007).

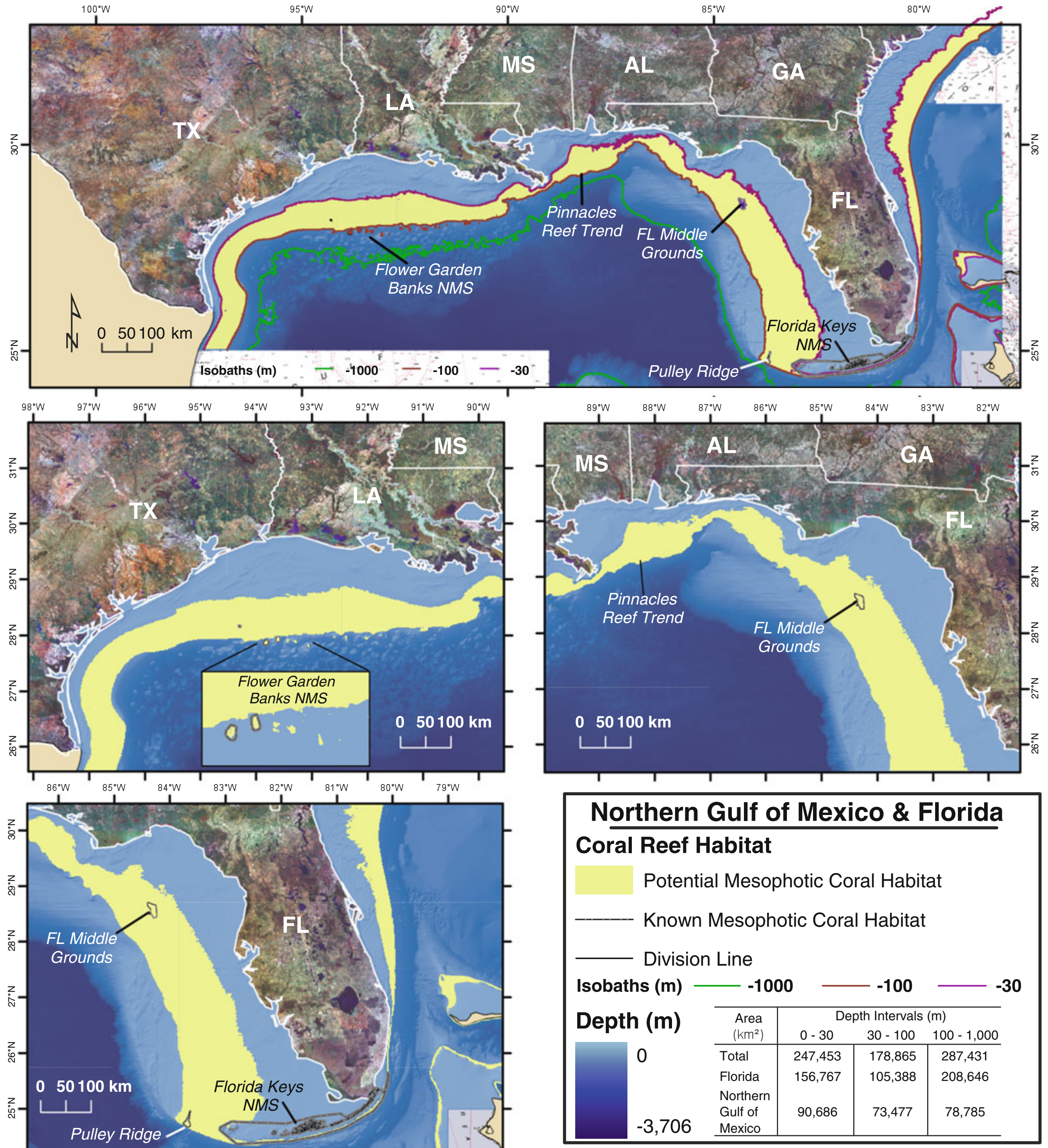


Fig. 1 Potential mesophotic coral reef habitat for the northern Gulf of Mexico and Florida

Stressors that are known to negatively impact coral ecosystems include land-based sources of pollution, sedimentation, and nutrients; high water temperatures leading to bleaching events; and physical disturbance from wave action due to storm-surge. Of the three regions investigated in our analyses, MCE distance from shore decreased, from the northern Gulf of Mexico (67.77 km), Florida (56.55 km), US Caribbean (8.76 km), and main Hawaiian Islands (5.54 km). Comprehensive shallow-water coral ecosystem maps available for the main Hawaiian Islands

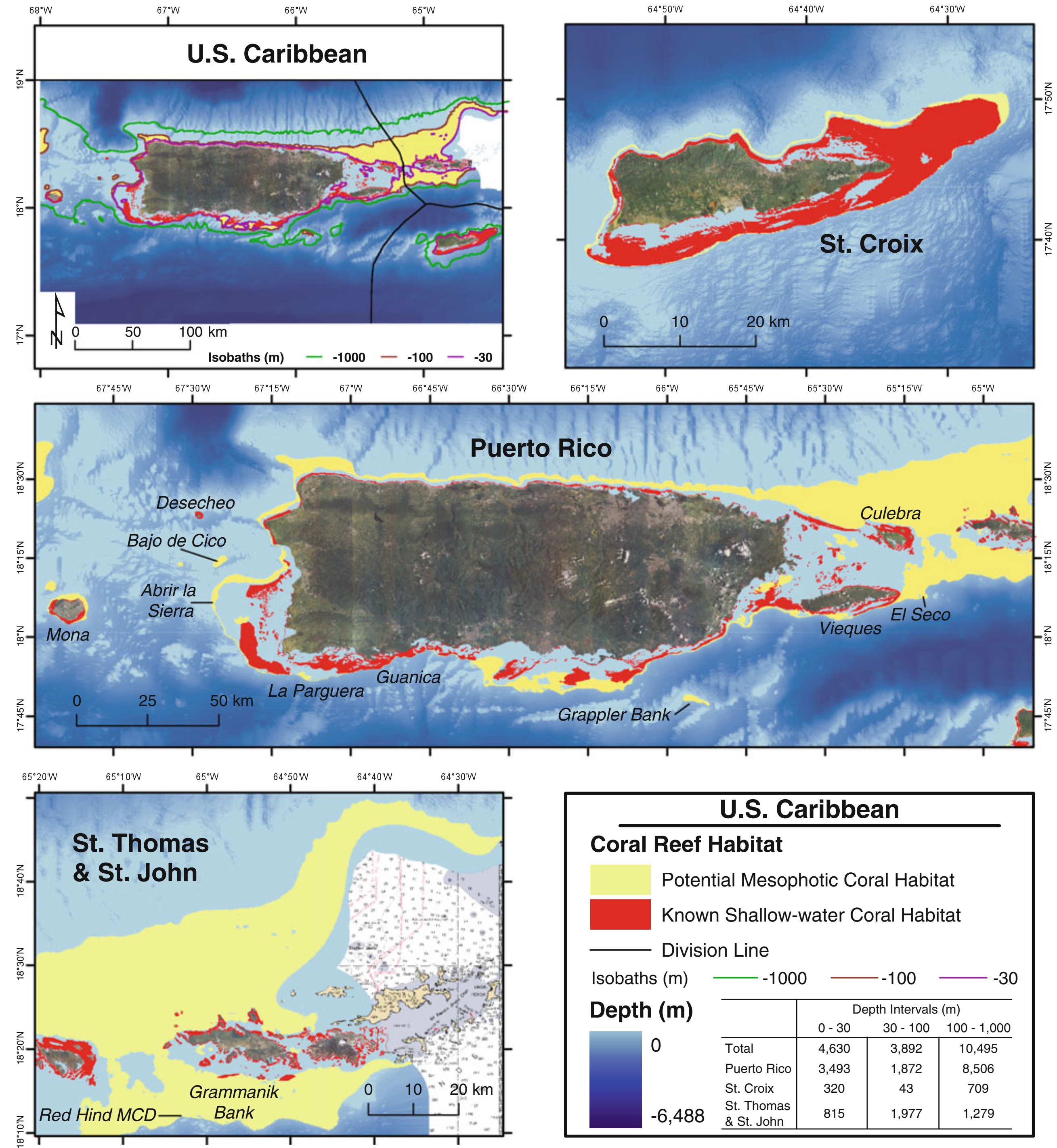
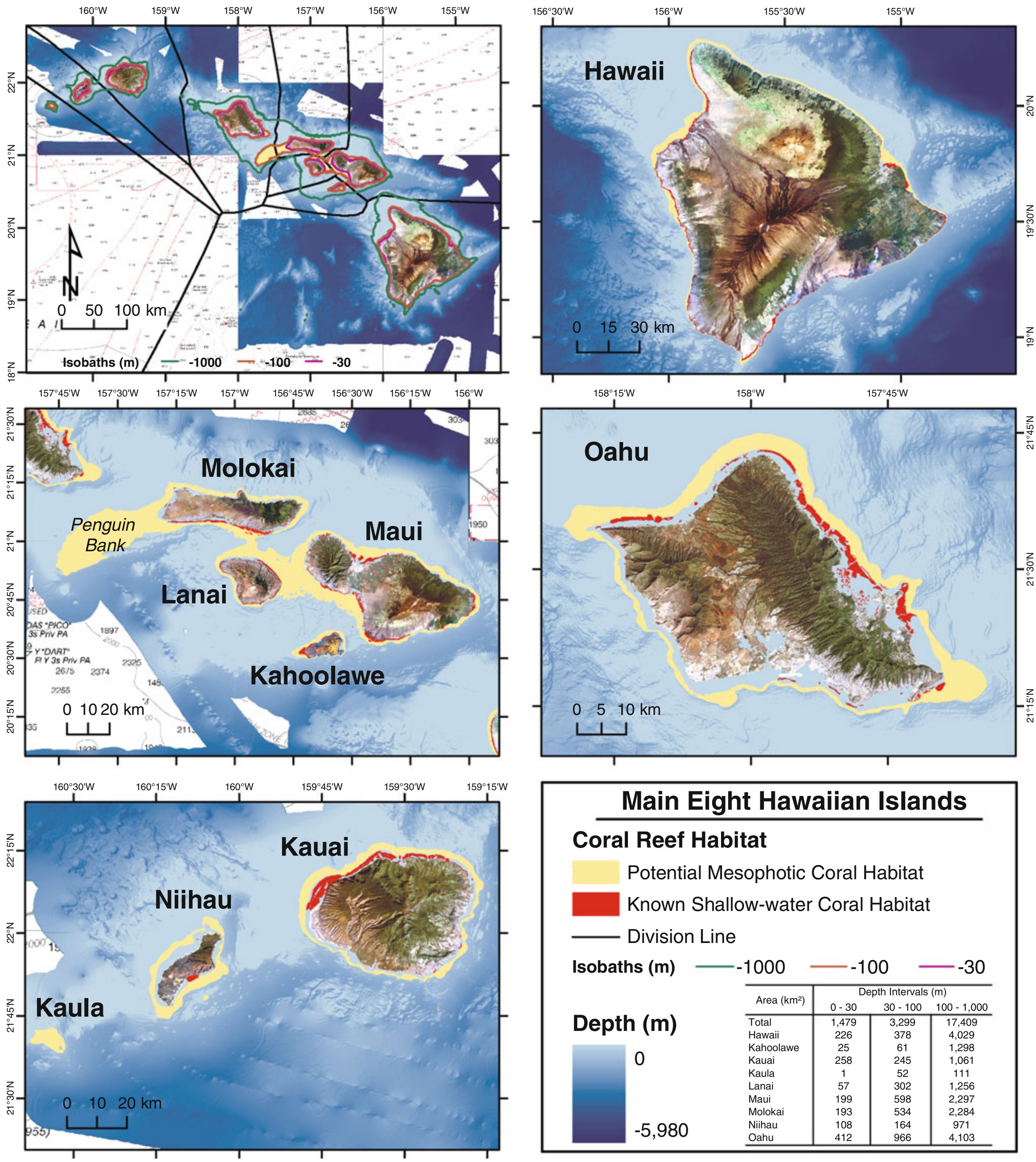


Fig. 2 Potential mesophotic coral reef habitat for the US Caribbean

and US Caribbean were used to calculate MCE distance to known shallow-water coral reefs (Battista et al. 2007; NOAA 2001). On average, potential MCE habitats in the Caribbean (9.66 km) were approximately 3 km closer to shallow-water reefs than those in the main Hawaiian Islands (6.20 km).

US Caribbean MCEs

The US Caribbean (excluding Navassa) encompasses the islands of Puerto Rico, Vieques, Culebra, St. Thomas, St. John, and St. Croix. The total potential MCE habitat within the insular shelf and slope areas is 3,892 km^2 (46%)



Area (km²)	Depth Intervals (m)		
	0 - 30	30 - 100	100 - 1,000
Total	1,479	3,299	17,409
Hawaii	226	378	4,029
Kahoolawe	25	61	1,298
Kauai	258	245	1,061
Kaula	1	52	111
Lanai	57	302	1,256
Maui	199	598	2,297
Molokai	193	534	2,284
Niihau	108	164	971
Oahu	412	966	4,103

Fig. 3 Potential mesophotic coral reef habitat for the main Hawaiian Islands

(Fig. 2). MCE habitats in the US Caribbean can be divided into two broad categories, low-gradient platforms (i.e., insular shelves and banks) and high-gradient slopes. At present, the basic geomorphology, benthic community structure, and distribution of MCEs in the US Caribbean remain largely unknown (although see García-Sais (2010), Smith et al. (2010), and Sherman et al. (2010) for site-specific studies).

Mapping of MCEs in the US Caribbean

In recent years, the Seabed autonomous underwater vehicle (AUV) has been used to map MCE's in the US Virgin Islands and Puerto Rico (Armstrong et al. 2002, 2006, 2009; Singh et al. 2004; Armstrong 2007; Rivero-Calle et al. 2009). At the Hind Bank Marine Conservation District (MCD), south of St. Thomas, US Virgin Islands, four, 1-km long photo transects provided quantitative data on benthic species composition and abundance at depths of 32–54 m. Within the western side of the MCD, well-developed MCEs with 43% mean living coral cover were found at depths of 40–47 m (Armstrong et al. 2006). These long (km-scale) photo transects have provided the first large-scale effort to map and characterize MCEs using high-resolution optical imagery. Information on Seabed capabilities and sensors can be found in Singh et al. (2004) and Armstrong and Singh (2006).

In Puerto Rico, diving surveys of the sessile-benthic and fish communities to depths of 50 m have been conducted in Isla Desecheo Bajo de Cico and Vieques (García-Sais et al. 2008; García-Sais 2010). At Isla Desecheo and Bajo de Cico, accumulations of rhodoliths have developed along low topographic relief terraces colonized by sponges of the genus *Agelas* spp. and *Aplysina* spp., the encrusting brown algae *Lobophora variegata*, and corals (13% cover, mostly *Agaricia lamarcki* and *A. grahamae*), at depths of 40–70 m (Fig. 4; García-Sais et al. 2008). Recent surveys by the Seabed AUV have documented large (up to ~1 m in diameter) encrusting colonies of *Agaricia* spp. to depths of approximately 100 m in Isla Desecheo.

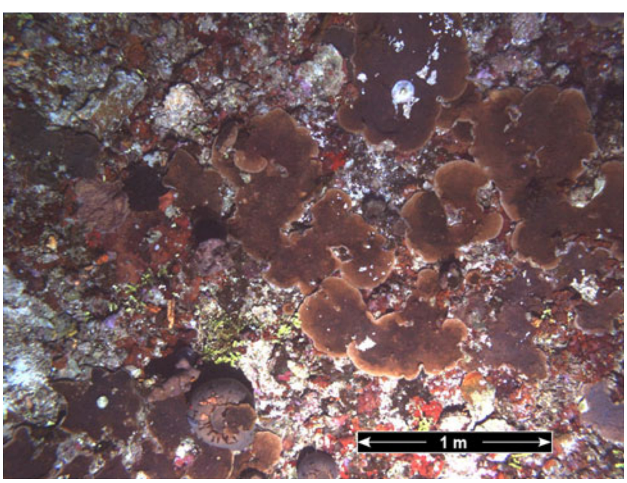


Fig. 4 Healthy colonies of the genus *Agaricia* can be found at depths of 70 m or more in Bajo de Cico and Isla Desecheo, western Puerto Rico. This image was obtained by the Seabed AUV in 2008 at a depth of 72 m and from an altitude of 3 m

Platforms

Low-gradient platform MCE habitats include outer insular shelves that dip gently into mesophotic depths and more isolated banks with relatively flat tops that rise into the mesophotic zone. These well-developed and structurally complex MCEs occur in very clear water and are dominated by a flattened-plate morphotype of *Montastraea annularis* complex, with *Agaricia lamarki*, *A. grahamae,* and *Porites astreoides* also common (Nemeth et al. 2004; Armstrong et al. 2006; García-Sais et al. 2008; Smith et al. 2010); in Puerto Rico and USVI, these communities have been reported down to depths of ~50 m.

Deep insular shelf MCEs cover large areas of the Puerto Rico—USVI platform between the islands of St. Thomas, Culebra, and Vieques (Fig. 2). MCEs of this type have been described on the outer shelf south of Vieques at depths of 36–43 m (García-Sais et al. 2008; Rivero-Calle et al. 2009) and on the broad insular shelf that stretches south of St. Thomas and St. John in the US Virgin Islands (Nemeth et al. 2004; Armstrong et al. 2006; Smith et al. 2010). The shelf south of St. Thomas and St. John dips gently southward reaching depths of 50–60 m before reaching a rimmed shelf edge that rises to depths of between ~30 and 50 m. Well-developed MCEs at water depths of between ~30 and 50 m with coral cover of >40% have been documented in this region (Armstrong et al. 2006). The geomorphology of this MCE habitat consists of a series of coral ridges ~100 m across aligned parallel to the 100-fathom contour. The ridges are separated from each other by sand-floored grooves ranging from 50 to 300 m wide.

Platform MCEs also include more isolated banks such as Bajo De Cico in the Mona passage. Aside from a narrow ridge in the southwest corner, the top of this feature consists of a planar surface that dips gently from ~40 m down to ~90 m water depth before dropping abruptly to greater depths. Preliminary surveys indicate that much of this surface contains MCEs (García-Sais et al. 2008). Grappler Bank south of Puerto Rico is another isolated bank with high potential for MCEs and warrants future research and exploration.

Platforms, and smaller scale terraces along slopes, often contain extensive deposits of rhodoliths, which are concentrically encrusted nodules of red (coralline) algae (Bosellini and Ginsburg 1971). The rhodoliths are typically colonized by encrusting brown algae (*Lobophora variegata*), large upright and branching sponges (e.g., *Agelas* spp. *Aplysina* spp.) and corals, primarily *Agaricia* spp. Rhodolith accumulations develop along low-relief, gently sloping terraces below 40 m depth have been described at Isla Desecheo and Bajo de Cico seamount (García-Sais et al. 2008; García-Sais 2010). Living benthic cover in these habitats can reach over 95%, with coral cover averaging about 13%.

Slopes

The morphology of many Caribbean MCEs has been described in studies focused on deep reef environments and relic reef structures on upper continental and insular slopes at locales in the Caribbean such as Belize (James and Ginsburg 1979), Jamaica (Goreau and Land 1974; Moore et al. 1976), Puerto Rico (Seiglie 1971), Barbados (Macintyre et al. 1991), and the Bahamas (Ginsburg et al. 1991; Grammer et al. 1993). These classic studies provide information on the physical character of these environments and the physical/geological processes that occur within them, which together exert a fundamental control on the occurrence and distribution of MCEs. In a general sense, slope habitats refer to the steep margins of insular shelves and banks that extend from the platform break to the adjacent basin. Although there is variability among these sites, there are some common geomorphic features, such as breaks in slope, submarine terraces, and relic reef structures, which are prime settings for MCEs. Additionally, the morphology of these slope environments directs downslope sediment transport (Hubbard 1992), which exerts a control on the occurrence and distribution of MCEs on a local scale. Understanding the basic physical parameters of these environments is crucial to a sound understanding of MCEs.

Slope MCEs at Isla Desecheo and Bajo de Cico seamount down to ∼40 m water depth have been quantitatively described (García-Sais et al. 2008; García-Sais 2010). At these sites, benthic cover was dominated by macroalgae, sponges, massive scleractinian corals, and sand. On the insular slope off southwestern Puerto Rico, Armstrong et al. (2002) and Singh et al. (2004) found that coral cover decreased from 24% at 25–30 m to less than 2% at 30–60 m. The shelf edge here has a buttressed-reef formation with channels extending along the slope, which descends at 43° in most places (Morelock et al. 1977). Recent surveys in this area confirmed that maximum coral cover in La Parguera and Guánica occurs at the shelf edge and decreases with depth along the upper insular slope (Armstrong et al. 2009). Small isolated coral colonies of *Agaricia* were found to depths of about 65 m at both sites. This agrees with Acevedo et al. (1989) who reported that corals were present to a depth of 70 m in La Parguera.

Sherman et al. (2010) divide the insular slope of southwest Puerto Rico into an upper slope and basal slope based on a pronounced change in geomorphic character at ∼160 m water depth. Whereas the upper slope is largely rocky and well-lithified, the basal slope is more of a sediment-covered talus slope. This transition from an upper rocky slope to basal sediment slope is common to many reef-rimmed margins in the Caribbean, though the depth of the transition is variable, occurring at depths of ∼105–150 m in Belize (James and Ginsburg 1979), ∼120 m off the north coast of Jamaica (Goreau and Land 1974; Moore et al. 1976), ∼140 m on the Great Bahama Bank (Ginsburg et al. 1991), and perhaps more than 2000 m off the north coast of St. Croix (Hubbard et al. 1990). Sherman et al. (2010) further subdivide the upper slope of southwest Puerto Rico into two zones separated by a prominent break in slope gradient at ∼90 m water depth. Zone I extends from the shelf break at ∼20 m water depth down to the break at 90 m. Zone II extends from 90 m to the transition to the basal slope at ∼160 m. This prominent break in slope gradient below the shelf break is also common to many Caribbean margins. This region typically contains lush mesophotic coral growth including sheet-like and plate-like forms of *Montastraea*, *Agaricia*, and *Mycetophyllia* (Goreau and Land 1974; James and Ginsburg 1979; Ginsburg et al. 1991).

Deep buttresses at depths of ∼45–65 m are also common on Caribbean slopes such as Belize (James and Ginsburg 1979), Jamaica (Goreau and Land 1974), and Puerto Rico (Sherman et al. 2010). The buttresses are similar to shallower, shelf-edge spur and groove in occurrence and orientation but are typically larger in scale and more widely spaced. In slope environments, mesophotic coral growth is concentrated on the deep buttresses. The topographically high buttresses provide suitable substrates elevated above the surrounding seafloor and, therefore, removed from the influence downslope sediment transport, which gets funneled into intervening grooves. Coral cover on deep buttresses can equal that on shallower, shelf-edge spurs above. Caves and notches are common along the seaward fronts and sides of the buttresses.

Beyond the deep buttresses, there is typically a steep escarpment that drops precipitously to the base of the upper slope at ∼120–160 m water depth (Goreau and Land 1974; Moore et al. 1976; James and Ginsburg 1979; Ginsburg et al. 1991; Sherman et al. 2010). At locales such as Belize and Jamaica, the escarpment starts at the seaward margin of the deep buttresses at depths of ∼65 m (Goreau and Land 1974; James and Ginsburg 1979). On the Great Bahama Bank, the escarpment starts as shallow as 30 m (Ginsburg et al. 1991), while off southwest Puerto Rico, it begins at ∼90 m water depth (Sherman et al. 2010). Off the north coast of St. Croix, the escarpment starts at between 30 and 80 m water depth and drops to depths of more than 2,000 m (Hubbard et al. 1990). The escarpment typically consists of a series of irregular and discontinuous ledges about a meter or so wide and mantled with fine sediment. Between the ledges, the walls are generally either bare rock or caves. Running down the wall perpendicular to the ledges are vertical fissures a few meters wide and several 10 s of meters long. The wall represents a biological transition zone from a benthic community of hermatypic corals, octocorals, green algae, and coralline algae to a deeper water community of coralline algae, octocorals, ahermatypic corals, demosponges, and sclerosponges. Hermatypic corals remain common down to depths of 70–80 m but become increasingly rare below these depths (James and Ginsburg 1979).

Relic reefs and terraces

Along continental and insular slopes around the Caribbean, submerged ridges and terraces occur at consistent depths and were likely formed at times during the late Quaternary when sea levels were below present. The most conspicuous of these are ridge and terrace features that occur at depths between ~50 and 90 m off the west coast of Barbados (Macintyre et al. 1991), the west and southwest coasts of Puerto Rico (Seiglie 1971; Sherman et al. 2010), western Guiana, and the north coast of Jamaica (Macintyre et al. 1991; Macintyre 2007 and references therein). These features can be a result of erosional processes (i.e., wave-cut platforms), constructional processes (i.e., relic reefs), or some combination of the two. Coring of a series of submerged ridges off the south coast of Barbados by Fairbanks (1989) indicates that, at this location, these features are relic shallow-water reefs consisting of a framework dominated by *Acropora palmata* and other shallow-water species. Based on radiometric dating of the Barbados cores, these relic features likely represent reef-constructed morphology drowned by rapid sea-level rise events associated with meltwater pulse 1A (~14 ka) and 1B (~11.3 ka) (Fairbanks 1989; Bard et al. 1990; Macintyre et al. 1991; Montaggioni 2005; Macintyre 2007; Beaman et al. 2008; Sherman et al. 2010). Of significance to MCEs is the fact that these relic structures can provide topographically high, hard substrates above downslope sediment movement and suitable for colonization by corals. Macintyre et al. (1991) found that the relic reef off Barbados is now covered by a rich assemblage of sponges, algae, and scattered corals. Coring of these features could provide long-term records of MCEs, paleoceanographic and paleoclimatic conditions, and the response of MCEs to changing environmental conditions.

MCEs in the Northern and Eastern Gulf of Mexico

The spatial extent of potential MCE habitat in the northern and eastern Gulf of Mexico (GOM), based the seafloor area between 30 and 100 m, is on the order of 20 times greater than that of the US Caribbean and main Hawaiian Islands combined (Figs. 1, 2, 3). The distributions of MCEs in the GOM are poorly known with respect to the potential areas of occurrence. Some well-known areas, such as the Florida Middle Grounds (carbonate/reefal banks) and Flower Garden Banks (salt diapir region of the northern Gulf), are large areas easily identified on bathymetric charts, having MCEs that have been investigated over the years due to their proximity to oil and gas operations or commercial and recreational fishing activities. A significant portion of this area, the west Florida Shelf, is a distally steepened carbonate-ramp (Read 1985), having a gently sloping seafloor and a poorly understood distribution of hardbottom and carbonate sediment cover. Efforts to better understand the response of sedimentary environments to Late Quaternary sea-level fluctuations across the west Florida Shelf have led to a realization of important linkages between relic, non-reefal, paleoshoreline structures and the occurrence of present-day MCEs, such as the Pulley Ridge MCE (Jarrett et al. 2005).

Northern Gulf of Mexico

In the northern GOM, the salt diapir region on the upper slope has created much suitable MCE habitat. The significant relief of these salt domes combined with suitable water conditions has resulted in MCE development on numerous structures (Flower Garden and other banks) with significant coral cover extending to approximately 50 m (Bright et al. 1985; Rezak et al. 1985; Precht et al. 2008). The depth range of these structures, from approximately 18 m to over 100 m, spans the full range of interest for MCEs. Long-term monitoring focused on west and east Banks have shown stability of coral communities and fish populations, with coral cover on the order of 50–60%. Dominant coral associations include a *Montastraea-Diploria-Porites* Zone (<36 m) and deeper *Stephanocoenia-Millepora* Zone (36–52 m) (Precht et al. 2008). The spatial extent of these MCEs is limited—the largest areas being west and east Garden Banks covering 137 and 67 km^2, respectively (Precht et al. 2008). The deeper areas between the dome structures may exhibit hardbottom habitat such as patch reefs, ridges, and scarps that may provide important connectivity between banks (Schmahl et al. 2008).

Northeastern and Eastern Gulf of Mexico

Throughout the northeast and eastern areas of the GOM, MCE habitat is largely related to drowned coral/algal banks or pinnacles, and paleoshoreline structures, both products of the timing and magnitude of Late Quaternary sea-level history (Ludwick and Walton 1957; Schroeder et al. 1988; Locker et al. 1996; Mallinson et al. 2003; Hine et al. 2008).

In the Pinnacles Reef Trend of the northeastern GOM, drowned Late Pleistocene to Early Holocene reef complexes in 70–100 m no longer support living hermatypic coral communities, although important mesophotic communities are present including ahermatypic scleractinian corals, octocorals, antipatharian corals, bryozoans, sponges, and reef-fish communities (Gardner et al. 2000; Weaver et al. 2002). The depth range of these structures is coincident with the range of paleoshoreline features rimming Florida in these water depths (Locker et al. 1996; Jarrett et al. 2005); thus, there may be other features of this nature in more suitable locations further to the south for MCE development. Lowstand deltas in the northeastern GOM having secondary features such as mounds and ridges may reflect similar shallow-water environments drowned during deglacial sea-level rise (Gardner et al. 2005). It is likely that water conditions more favorable to MCE habitat would improved with distance from the Mississippi River inflow.

The Florida Middle Grounds (FMG) is a grouping of carbonate banks in 24–45 m water depth in the northern portion of the west Florida Shelf, which are believed to represent Late Quaternary reef buildups, including Holocene reefs that were unable to keep pace with rising sea level (Ludwick and Walton 1957; Brooks and Doyle 1991; Mallinson et al. 2003; Hine et al. 2008). Various bank morphologies have been documented by multibeam mapping that range from groups of banks greater than a few km in scale to smaller patch reefs <1 km in diameter (Hine et al. 2008). These banks support diverse living MCE communities, albeit somewhat reduced in richness perhaps due to incursions of cooler water or plumes of water from fluvial sources, such as Mississippi River runoff, that can subject the area to cold low-salinity water with high turbidity and nutrients/pollution (see review by Hine et al. 2008). Coral species include abundant Milleporina (up to 32% cover) and over 18 species of Scleractinia (Grimm and Hopkins 1977; Hopkins et al. 1977).

Southeast Gulf of Mexico

At the south end of the west Florida Shelf, a variety of carbonate banks and paleoshoreline structures reflect periods of reef or shoreline building during the Late Quaternary that were drowned by very rapid sea-level rise events, leaving behind reef edifices and paleoshorelines preserved by rapid flooding. Reefal banks in the Tortugas region share a similar history of development and depth range with the FMG (Mallinson et al. 2003). Portions of Tortugas Bank including the Sherwood Forest reef terrace (Franklin et al. 2003) and Riley's Hump (Weaver et al. 2006) support coral communities dominated by scleractinian coral assemblages with coverages up to 28% and reaching down to 50 m depth (see Fig. 5 for locations). In deeper water west of the Tortugas, the main topographic forms are Late Pleistocene paleoshorelines, beach and ridge environments or drowned barrier islands such as southern Pulley Ridge, which now support MCEs (Cross et al. 2005; Jarrett et al. 2005). The MCE at Pulley Ridge appears to be quite thin and/or uniform, since the original barrier-island morphology does not appear to be noticeably altered by the overlying MCE. The coral communities of Pulley Ridge are documented from 60 to 75 m water depth (Cross et al. 2005). Multibeam mapping of drowned shoreline ridge complexes west of Pulley Ridge extending to 100 m water depth (David Naar pers. comm.), and video transects suggesting "pinnacles" structures in 150 m water depth (Phillips et al. 1990), indicate suitable structure is present, yet the associated occurrence of MCEs is unknown (Fig. 5). Additionally, along the bank margin south of Riley's Hump lies Miller's Ledge, an escarpment with ~40 m relief in 84–124 m water depth is characterized by an encrusting assemblage dominated by sponges, bryozoans, small solitary corals, and sea whips (Weaver et al. 2006). The large expanse of shelf/slope area between the Tortugas/Pulley Ridge area and the FMG is poorly mapped. Following on the assumption that the paleoshoreline development occurred at specific elevations related to possible sea-level stillstand events (Locker et al. 1996), reconnaissance mapping has found additional shoreline structures extending well to the north of Pulley Ridge, suggesting that much potential MCE habitat remains to be discovered (Fig. 5).

MCEs in the Pacific: examples from Hawaii, American Samoa, and the Commonwealth of the Northern Mariana Islands

Until recently, little effort has been made to systematically identify, map, and study scleractinian coral reefs found at depths below ~30 m in the Pacific Ocean. Although understudied relative to shallow reefs, these deeper reefs can have higher coral densities and cover percentages. A total of 611 km of seafloor video have been collected, usually at mesophotic depths, on most of the islands and many submerged banks across the islands of American Samoa and the Hawaiian and Mariana Archipelagos. This section discusses the insights this dataset provides regarding MCEs in these widely separated areas of the tropical Pacific. MCEs at depths from 30 m to at least 100 m are found in the Samoan and Mariana Archipelagos, have been found as deep at 130 m in Hawaii and are probably that deep in the other archipelagos as well. The available data suggest that MCEs are more common in the Samoan than in the Mariana and Hawaiian Islands. Coral species

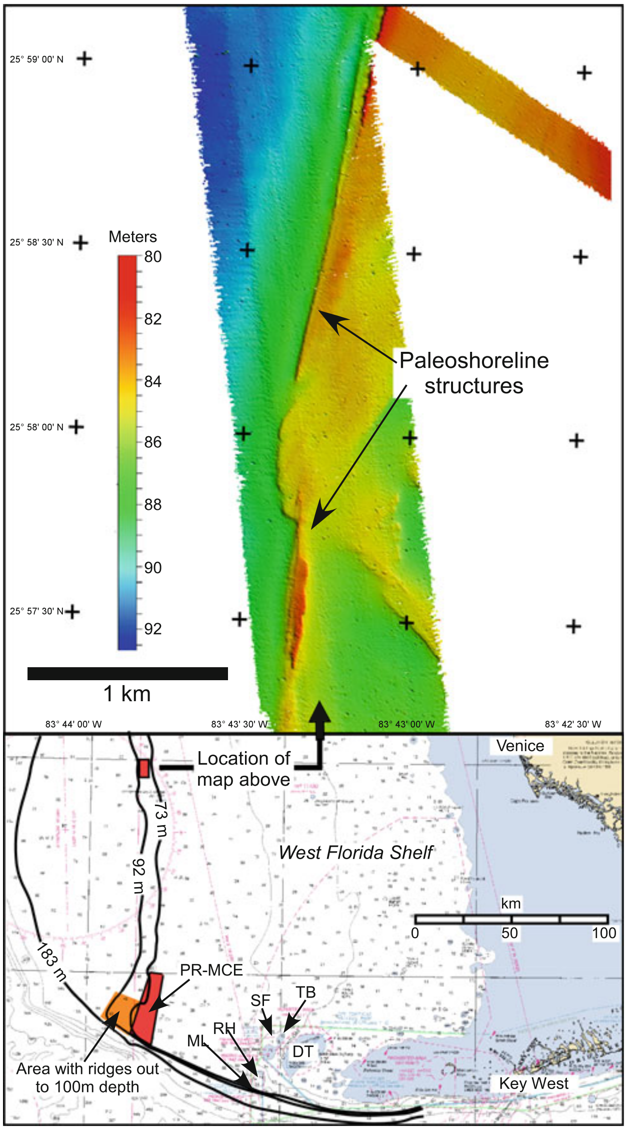


Fig. 5 Multibeam bathymetry (*top panel*) from the southern region of the west Florida Shelf showing paleoshoreline structures that may extend over large distances and at specific depths (unpublished data courtesy of David Naar and Brian Donahue). These topographic ridges provide potential MCE substrate, but their locations are poorly known. (PR-MCE = Pulley Ridge MCE; DT = Dry Tortugas National Park; TB = Tortugas Bank; SF = Sherwood Forest; RH = Riley's Hump; ML = Miller's Ledge)

diversity appears to decline with increasing depth, and the percentage of seafloor colonized by living corals, other invertebrates, and macroalgae declines markedly between depths of 60 and 90 m, while the proportion of uncolonized hard substrate increases.

Hawaiian Archipelago

Perhaps the best-known MCE within these island groups is located in the Au'au Channel between the Hawaiian Islands of Maui and Lanai (Fig. 6). Multibeam maps of this area (Torresan and Gardner 2000) reveal a karstic topography that was subaerially exposed during late Quaternary sea-level fluctuations, with Holocene reef growth occurring as a thin veneer on topographic highs (Grigg et al. 2002). Kahng and Maragos (2006) report that for several areas in the main Hawaiian Islands (MHI), including the Au'au Channel, *Leptoseris* sp. corals dominate hard substrata below 60 m, exceed 90% cover in places, and are found as deep as 153 m. Living benthic cover generally declines descending from depths of 50–140 m in the Au'au Channel, and different suites of benthic organisms dominate hard substrates at specific depths within that zone (Kahng and Kelley 2007).

Mesophotic corals have been found at both ends of the Hawaiian Archipelago as well as on many of the islands in between (Fig. 6), suggesting that all Hawaiian Islands and atolls appear to have the potential to host MCEs. However, it appears that MCEs are generally better developed and found deeper at the southeastern end of the Archipelago.

Rooney et al. (2010) report that, in addition to shallow reefs, different types of MCEs are found in Hawaii. The distribution of each is hypothesized to be controlled by a suite of physical factors and characterized by unique community structure. MCEs are classified as one of the following general types: Upper mesophotic MCEs are found at depths from ca. 30 to 50 m and are dominated by corals found in shallow reefs but generally have lower species diversity. MCE growth in this zone is sheltered by depth from damage due to seasonal high wave events. Branching/Plate Coral MCEs are found at depths of ca. 50–80 m and tend to be clearly dominated by coral colonies of one morphology. *Leptoseris* sp. coral MCEs are most common from depths of ca. 80 m to at least 130 m and are hypothesized to be most common on banks and coastlines oriented to catch the maximum annual insolation, and with unusually clear water conditions.

Preferred substrate for Hawaiian MCEs appears to be on rock structures elevated above sediment deposits and includes sea-level terraces formed by late Quaternary sea-level fluctuations (Fletcher and Sherman 1995; Fletcher et al. 2008; Rooney et al. 2008). In the Au'au Channel, MCEs are situated on solution rims and other elevated portions of the karstified limestone platform. Elevated outcrops of tuff formed from rift-zone volcanism found around some of the MHI have been found, in some cases at least, to support MCEs.

Mariana Archipelago

The Garapan Anchorage on the west side of the island of Saipan is located on a marine terrace, probably composed of the Pliocene Mariana Limestone (Riegl et al. 2008), at

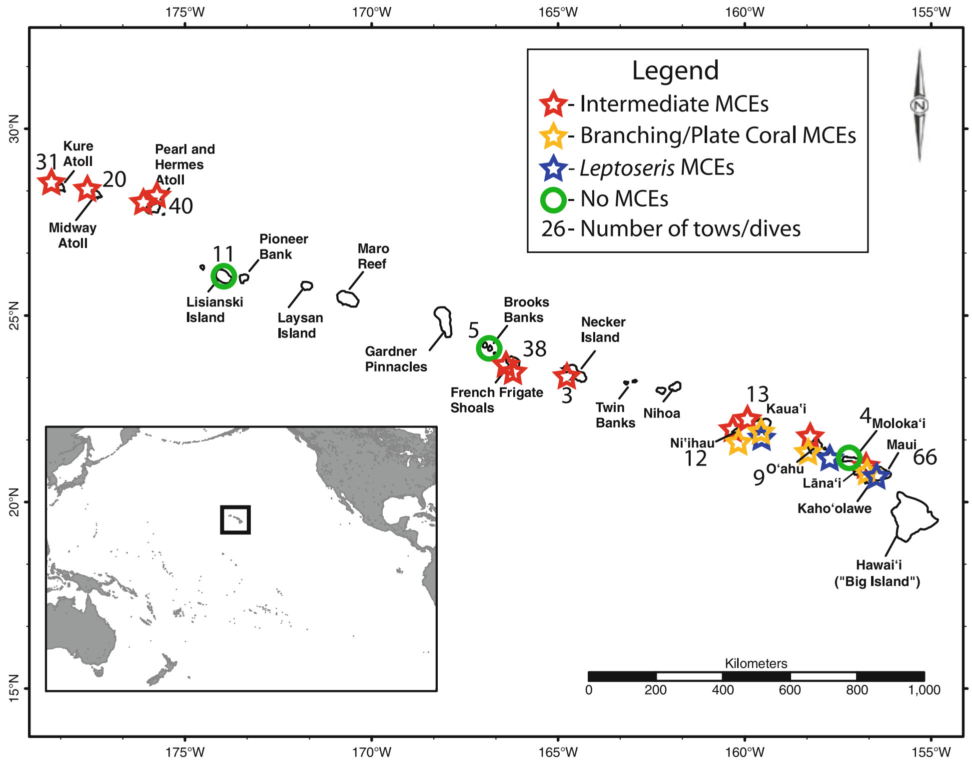


Fig. 6 Mesophotic coral ecosystems known to date from the Hawaiian Islands. Locations of different types of MCEs are shown with color coded stars and areas where imagery from multiple camera sled deployments has been collected. Areas where no MCEs have been found are shown within the green circles. From Rooney et al. (2010)

depths of ca. 20–50 m (Fig. 7). It is the largest shallow insular shelf (58 km^2) in the entire Mariana Archipelago, making it a unique site, both for anchoring large vessels and as MCE habitat. Except in areas normally used for anchoring, numerous patches of intermediate depth MCEs are found. A large MCE of *Euphyllia paraancora* corals discovered here correlates with the branching/plate coral MCEs of Hawaii.

The southern islands of the archipelago are older, usually capped with limestone, and with generally better developed shelves (Riegl et al. 2008). The northern islands are younger, often very steep, and some are still active volcanoes. Although corals at mesophotic depths were found on 11 islands and banks, more work is needed to better understand the distribution of MCEs and their linkages with shallow reefs. Surveys throughout the archipelago confirm the uniqueness of the MCE complex on the shelf where the Garapan Anchorage is located.

American Samoa

Tutuila, the largest island in American Samoa, hosts a number of MCEs on its insular shelf (Bare et al. 2010). The Manua Islands of Ofu, Olosega, and Ta'u are 100 km east of Tutuila, lightly populated, younger than Tutuila, and also part of the Samoan chain of hotspot volcanoes. Ofu and Olosega are only 75 m apart and are connected by a bridge. A total of 16 camera sled tows each have been completed in the vicinity of Ta'u and Ofu-Olosega. Approximately 65% of the tows reveal mesophotic corals. MCEs are found at each of the islands at depths from 30 to 80 m, often include high coral cover, and are most common on flat-topped ridges extending out from island corners. MCEs around Tutuila are concentrated on a series of banks lining the seaward edge of the island's extensive insular shelf, which are hypothesized to be relict barrier reef features (Bare et al. 2010). The top of a volcanic cone 2.3 km from Ta'u is also heavily colonized by a particularly dense and diverse coral community.

Methodologies for sampling and mapping MCEs

MCEs pose significant challenges to sampling and mapping efforts. Their nominal 30–100 m depth range places them at the limit of conventional scuba diving and beyond the scope of airborne and satellite remote-sensing instrumentation. As a result, most MCE investigations have involved extending shallow-water techniques and/or utilizing deep-sea technology to investigate this depth realm. This section presents a brief discussion of some of the more relevant technologies suitable to sample or map MCEs.

Acoustic technologies

Assorted acoustic-based instruments have been used to investigate coral formations in the mesophotic zone. The

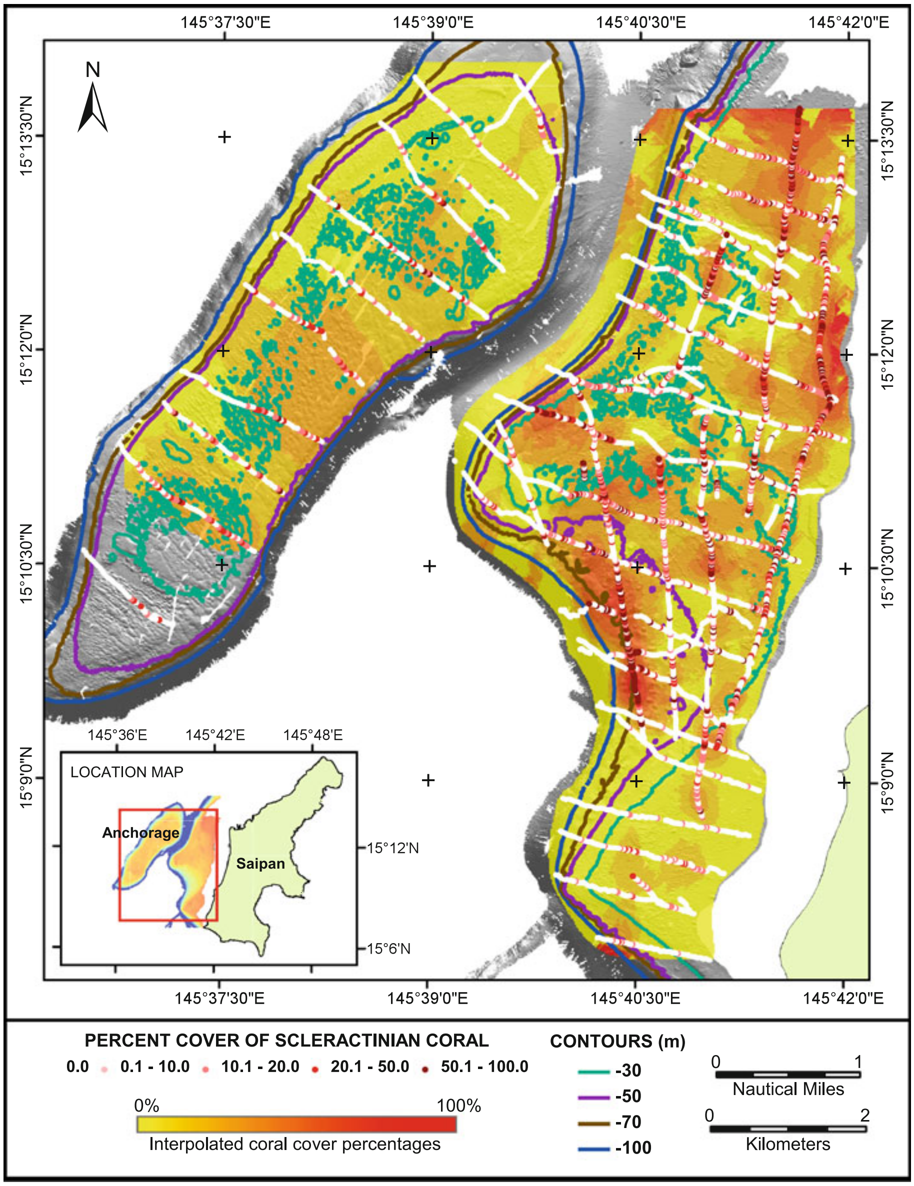


Fig. 7 Garapan Anchorage of the western coast of Saipan, CNMI. Camera sled tracks are *color* coded to indicate percentages of coral cover and are overlain on a grid of coral cover interpolated from the camera sled data

most common and useful systems are swath-mapping systems, such as multibeam and side-scan sonar, which facilitate the mapping of large areas. These sonars transmit and receive a fan of narrow acoustic beams perpendicular to the direction of the transducer-head movement (Miller et al. 2006). Multibeam systems can provide acoustic backscatter imagery; however, the resolution is often not comparable to side-scan sonar. More recently, interferometric and multi-angle swath-bathymetry side-scan-sonar systems have been developed that acquire both high-quality backscatter and swath bathymetry using multiple transducer arrays that compute water depth using phase offsets and angle of return (Kraeutner et al. 2002; Gostnell 2005).

Sub-bottom profiling systems are very useful to understand the geologic framework within and around MCE habitat. The rocky nature of MCEs usually limits the usefulness of single-frequency transducers or swept-frequency Chirp sonar systems that employ high frequencies that provide limited to no penetration in hard substrate. Seismic-reflection profilers that employ more powerful broad-band frequency content <1 kHz, such as electromechanical "boomers" or small air and water guns, are better suited for MCE investigations.

Optical technologies

Underwater still and video cameras have become a core technology for most mesophotic studies (e.g., Strasburg et al. 1968; Liddell and Ohlhorst 1988; Pyle 2000; Vize 2006). Given the low-light levels and inaccessibility by airborne and spaceborne remote sensing, in situ photography and videography are the most effective means of acquiring the high-resolution imagery needed to characterize and monitor MCE habitats, as well as ground-truth associated acoustic data (Pyle 2000; Jarrett et al. 2005; Armstrong and Singh 2006; Armstrong et al. 2006; Menza et al. 2007; Gleason et al. 2010).

Emerging technologies

Promising advances in underwater imaging systems include pulsed-laser line imaging that can construct a 3D digital representation of the seafloor with spatial resolutions finer than 3 cm and laser line scanning (LLS) with spatial resolutions of 2–5 mm and multispectral imaging able to measure fluorescence (Leathern and Coles 1993; Moore et al. 2000; Jaffe et al. 2001; Mazel et al. 2003). These types of system have demonstrated the potential for reef classification, habitat mapping, and assessment based on fluorescence signatures. Continuing innovations in laser design are close to making compact, battery-powered LLS systems a viable mapping tool (Jaffe et al. 2001). Potter (2008) discusses a number of other underwater acoustic technologies in advanced stages of development, including (1) passive-phase conjugation, which allows both bathymetry and sub-bottom profiles to be retrieved from ambient noise in the ocean; (2) synthetic-aperture sonar, which produces acoustic images of higher resolution than that attainable with side-scan systems; and (3) diver-based multibeam sonar, which enables the collection of bathymetry for areas difficult to access from other deployment platforms.

Submerged mapping platforms

Tethered remotely operated vehicles (ROVs), autonomous underwater vehicles (AUVs), and towed vehicles or sleds offer a range of options for MCE mapping and sampling. ROVs have been used extensively and can be equipped with a variety of instruments, including cameras, multibeam and interferometric sonars, imaging tools, and environmental sensors (e.g., for light level, salinity, and temperature). However, ROVs provide limited coverage and are best for benthic characterizations. AUVs are becoming a more accessible platform capable of detailed mapping of MCEs. These untethered, battery-powered platforms follow programmed trajectories. A variety of oceanographic instruments is available in configurations compatible with AUV power and size limitations, including hydrographic sensors, cameras, sonars (interferometric, multibeam, and side-scan), and seismic profilers (Nicholson and Healey 2008). AUVs have been used to survey MCEs in Puerto Rico (Armstrong et al. 2002, 2009; Singh et al. 2004; Rivero-Calle et al. 2009) and the US Virgin Islands (Armstrong et al. 2006; Armstrong 2007).

One group of instrument-deployment platforms that has not been widely utilized for MCE research is towed vehicles. Most systems are capable of following a programmed flight path such as the Acrobat by Sea Sciences, Inc., and some units such as the TRIAXUS by MacArtney A/S can maintain a fixed altitude above the bottom, which is useful for high-resolution mapping. Another experimental system for mapping coral reef habitats is the Deep Along-Track Reef-Imaging System (ATRIS) developed by the US Geological Survey and based on the Sea Sciences Acrobat (Zawada et al. 2008). Deep ATRIS can acquire full-color digital images at 9 Hz and utilizes forward-looking sonar to minimize the risk of a collision.

Discussion

Geomorphology can exert a fundamental control on the occurrence and distribution of MCEs by providing favorable hard substrates for colonization and by directing the down-slope transport of sediment. Although unique settings such as volcanic ridges or salt domes may provide a foundation for MCEs, the role of past sea-level change has played a key role in forming antecedent topography which MCEs occupy. A common theme in most locations that affects MCE habitat is sea-level history and associated antecedent topography. Paleo coral reef morphologies, paleoshorelines, and erosional scarps and raised terraces are prime sites for MCE colonization by limiting the impact of sedimentation or turbid bottom water (Kahng et al. 2010). Along insular and continental slope environments, common features, such as breaks in slope, submarine terraces, and relic reef structures, are prime locations for MCEs and represent important targets for future study. Deep shelf environments represent another important target because of the potentially large areas suitable for MCEs, as opposed to the relatively narrow zones that occur along steep slopes. Relic reefs and terraces formed during the late Quaternary at sea levels below present can provide favorable substrates for MCE formation and can also contain important records of late Quaternary ecologic, oceanographic, and climatic change.

On insular shelves, the tendency for steeper slopes favors preservation of erosional features such as terraces. On the low-gradient continental shelve such as the west Florida Shelf, the predominant topography results from depositional/accretional processes (banks and paleoshorelines). Hence, the morphology of MCEs is largely inherited from a suite of pre-existing structures of highly diverse origins. Deep insular shelf settings offer several unique advantages that allow coral communities to flourish. These settings are typically located far from any sources of terrestrial runoff, resulting in high water transparency and little or no sediment stress. Their remote location also isolates them from most anthropogenic influences. These MCEs occur deep enough to avoid storm-induced wave damage (Armstrong et al. 2006; Rivero-Calle et al. 2009). Because of their importance as a spatially extensive setting for MCEs, as habitat and spawning grounds for fish (Nemeth 2005) and their potential as refuge areas (Riegl and Piller 2003; Armstrong et al. 2006), there is a critical need to map, monitor, and study these deep insular shelf settings.

The single most important issue from a mapping perspective is the lack of knowledge on the potential extent of MCEs. This challenge involves both identification of potential sites (suitable topography) and in situ observations for ground truthing. Rooney et al. (2010) note that the rate of discovery of MCEs in the Hawaiian Chain is approximately correlated with the level of effort. In areas such as the west Florida Shelf, so little is known about the occurrence of MCEs that the main concern begins with locating potential sites based on topographic surveys.

Supporting these mapping objectives will require utilization of both established and new technologies. The mapping approaches could use a nested-scale approach, mapping large areas to locate potential structure (e.g., Rooney et al. 2010; Bare et al. 2010), followed by smaller scale investigations. Some consideration should be given to predictability of depths, by which known sea-level events, including past sea-level highstands, or changing rates of recent sea-level rise, developed structures for MCE sites (see Sherman et al. 2010). In addition to mapping, coring of mesophotic coral ecosystems is a critical research need for providing long-term, millennial-scale records against which the current state of shallow reefs may be compared. Due to slow growth rates, it may be assumed that MCE communities are generally thin deposits that do little to change the antecedent morphology (Jarrett et al. 2005). In some areas, shallow-water coral ecosystems may undergo transition to MCEs (e.g., García-Sais 2010). Alternatively, some MCEs might only be initiated at mesophotic depths when sea-level rise and shoreline transgression have resulted in sufficient isolation, or protection, from near-shore environmental impacts. The potential thickness associated with these styles of development is unknown. Coring studies would provide important information on the accretion history of these systems, including their initiation, how they have changed over time in response to sea level or other environmental parameters, and how they may be impacted by current and predicted environmental changes.

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References

Acevedo R, Morelock J, Olivieri RA (1989) Modification of coral reef zonation by terrigenous sediment stress. Palaios 4:92–100

Armstrong RA (2007) Deep zooxanthellate coral reefs of the Puerto Rico—U.S. Virgin Islands insular platform. Coral Reefs 26:945

Armstrong RA, Singh H (2006) Remote sensing of deep coral reefs in Puerto Rico and the U.S. Virgin Islands using the seabed autonomous underwater vehicle. SPIE Europe remote sensing conference proceedings #6360-10, pp A-1 to A-8

Armstrong RA, Singh H, Torres J (2002) Benthic survey of insular slope coral reefs using the SeaBED AUV. Backscatter 13:22–25

Armstrong RA, Singh H, Torres J, Nemeth R, Can A, Roman C, Eustice R, Riggs L, García-Moliner G (2006) Characterizing the deep insular shelf coral reef habitat of the Hind Bank marine conservation district (U.S. Virgin Islands) using the SeaBED autonomous underwater vehicle. Cont Shelf Res 26:194–205

Armstrong RA, Cardona M, Singh H, Rivero-Calle S, Gilbes F (2009) Monitoring coral reefs in optically-deep waters. Proc 11th Int Coral Reef Symp: 593–597

Bard E, Hamelin B, Fairbanks RG, Zindler A (1990) Calibration of the 14C timescale over the past 30, 000 years using mass spectrometric U-Th ages from Barbados corals. Nature 345: 405–410

Bare AY, Grimshaw KL, Rooney JJ, Sabater MG, Fenner D, Carroll B (2010) Mesophotic communities of the insular shelf at Tutuila, American Samoa. Coral Reefs 29 (this issue). doi:10.1007/s00338-010-0600-y

Battista TA, Costa BM, Anderson SM (2007) Shallow-water benthic habitats of the main eight Hawaiian islands (DVD). NOAA Technical Memorandum NOS NCCOS 61, Biogeography Branch. Silver Spring, MD. Available from: http://ccma.nos.noaa.gov/products/biogeography/hawaii_cd_07/htm/overview.html

Beaman RJ, Webster JM, Wust RAJ (2008) New evidence for drowned shelf edge reefs in the Great Barrier Reef, Australia. Mar Geol 247:17

Bosellini A, Ginsburg RN (1971) Form and internal structure of recent algal nodules (rhodolites) from Bermuda. J Geol 79:669–682

Bright TJ, McGrail DW, Rezak R, Boland GS, Trippet AR (1985) The Flower Gardens: a compendium of information. OCS Study MMS 85–0024, U S Department of Interior Minerals Management Service, Gulf of Mexico. OCS Regional Office, New Orleans, p 103

Brooks GR, Doyle LJ (1991) Geologic development and depositional history of the Florida Middle Ground: a mid-shelf, temperate-zone reef system in the northeastern Gulf of Mexico. In: Osborne

RH (ed) From shoreline to abyss: contributions in marine geology in honor of Francis Parker Shepard. SEPM (Soc Sediment Geol) Spec Publ No 46, pp 189–203

Cross VA, Twichell DC, Halley RB, Ciembronowicz KT, Jarrett BD, Hammer-Klose ES, Hine AC, Locker SD, Naar DF (2005) GIS compilation of data collected from the Pulley Ridge deep coral reef region, Open-File Rep US Geol Surv 2005-1089

Divins DL, Metzger D (2008) NGDC coastal relief model, Volumes 3, 4, 5 9, and 10. Available from: http://www.ngdc.noaa.gov/mgg/coastal/coastal.html

Fairbanks RG (1989) A 17,000-year glacio-eustatic sea-level record: influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. Nature 342:637–642

Fletcher CH, Sherman C (1995) Submerged shorelines on Oahu, Hawaii: archive of episodic transgression during the deglaciation? J Coast Res Spec Issue 17:141–152

Fletcher CH, Conger CL, Engels M, Field M, Grossman EE, Harney JN, Murray-Wallace C, Rooney JJ, Rubin K (2008) Complex origin and structure of the Oahu carbonate shelf: Hawaiian Islands. In: Riegl BM, Dodge RE (eds) Coral reefs of the USA. Springer Science, ISBN 978-1-4020-6846-1, pp 435–487

Franklin EC, Ault JS, Smith SG, Luo J, Meester GA, Diaz GA, Chiappone M, Swanson DW, Miller SL, Bohnsack JA (2003) Benthic habitat mapping in the Tortugas Region, Florida. Mar Geodesy 26:19–34

García-Sais JR (2010) Reef habitats and associated sessile-benthic and fish assemblages across an euphotic–mesophotic depth gradient in Isla Desecheo, Puerto Rico. Coral Reefs 29 (this issue). doi:10.1007/s00338-009-0582-9

García-Sais JR, Appeldoorn R, Battista T, Bauer L, Bruckner A, Caldow C, Carrubba L, Corredor J, Diaz E, Lilyestrom C, García-Moliner G, Hernandez E, Menza C, Morell J, Pait A, Sabater J, Weil E, Williams E, Williams S (2008) The state of coral reef ecosystems of Puerto Rico. In: Waddell JE, Clarke AM (eds) The state of coral reef ecosystems of the United States and Pacific freely associated states: 2008. NOAA technical memorandum NOS NCCOS 73. NOAA/NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team, Silver Spring, MD, pp 75–116, Available from: http://ccma.nos.noaa.gov/ecosystems/coralreef/coral2008/welcome.html

Gardner JV, Sulak KJ, Dartnell P, Hellequin L, Calder B, Mayer LA (2000) Cruise report RV OCEAN SURVEYOR cruise O-1-00-GM, the bathymetry and acoustic backscatter of the Pinnacles area, northern Gulf of Mexico. Open-File Rep US Geol Surv 00-350

Gardner JV, Dartnell P, Mayer LA, Clarke JE, Calder BR, Duffy G (2005) Shelf-edge deltas and drowned barrier–island complexes on the northwest Florida outer continental shelf. Geomorphology 64:133–166

Ginsburg RN, Harris PM, Eberli GP, Swart PK (1991) The growth potential of a bypass margin, Great Bahama Bank. J Sediment Res 61:976–987

Gleason ACR, Gracias N, Lirman D, Gintert BE, Smith TB, Dick MC, Reid RP (2010) Landscape video mosaic from a mesophotic coral ecosystem. Coral Reefs 29 (this issue). doi:10.1007/s00338-009-0544-2

Goreau TF, Land LS (1974) Fore-reef morphology and depositional processes, north Jamaica. In: Laporte LF (ed) Reefs in time and space, Spec Publ No 18. SEPM (Soc Sediment Geol), Tulsa, pp 77–89

Gostnell C (2005) Efficacy of an interferometric sonar for hydrographic surveying: Do interferometers warrant an in-depth examination? Hydrogr J 118:17–24

Grammer GM, Ginsburg RN, Harris PM (1993) Timing of deposition, diagenesis, and failure of steep carbonate slopes in response to a high-amplitude/high-frequency fluctuation in sea level, Tongue of the Ocean, Bahamas. In: Loucks RG, Sarg JF (eds) Carbonate sequence stratigraphy: recent developments and applications, Am Assoc Pet Geol Mem 57, pp 107–131

Grigg RW, Grossman EE, Earle SA, Gittings SR, Lott D, McDonough J (2002) Drowned reefs and antecedent karst topography, Au'au Channel, S.E. Hawaiian Islands. Coral Reefs 21:73–82

Grimm D, Hopkins T (1977) Preliminary characterization of the octocorallian and scleractinian diversity at the Florida Middle Ground. Proc 3rd Int Coral Reef Symp 1:135–141

Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada DG, Appeldoorn R (2010) Theme section on "Mesophotic Coral Ecosystems: Characterization, Ecology, and Management". Coral Reefs 29 (this issue). doi:10.1007/s00338-010-0614-5

Hine AC, Halley RB, Locker SD, Jarrett BD, Jaap WC, Mallinson DJ, Ciembronowicz KT, Ogden NB, Donahue BT, Naar DF (2008) Chapter 4. Coral reefs, present and past, on the West Florida shelf and platform margin. In: Riegl BM, Dodge RE (eds) Coral reefs of the USA. Springer Science, Berlin, pp 125–171

Hopkins TS, Blizzard DR, Brawley SA, Earle SA, Grimm DE, Gilbert DK, Johnson PG, Livingston EH, Lutz CH, Shaw JK, Shaw BB (1977) A preliminary characterization of the biotic components of composite strip transects on the Florida Middle Grounds, northeastern Gulf of Mexico. Proc 3rd Int Coral Reef Symp 1:31–37

Hubbard DK (1992) Hurricane-induced sediment transport in open-shelf tropical systems–an example from St Croix, U.S. Virgin Islands. J Sediment Petrol 62:946–960

Hubbard DK, Miller AI, Scaturo D (1990) Production and cycling of calcium carbonate in a shelf-edge reef system (St Croix, U.S. Virgin Islands): applications to the nature of reef systems in the fossil record. J Sediment Petrol 60:335–360

Jaffe JS, Moore KD, McLean J, Strand MP (2001) Underwater optical imaging: status and prospects. Oceanography 14:64–75

James NP, Ginsburg RN (1979) The seaward margin of the Belize barrier and atoll reefs: special publication 3 of the IAS, Blackwell Scientific Publications, ISBN: 978-0-632-00523-9

Jarrett BD, Hine AC, Halley RB, Naar DF, Locker SD, Neumann AC, Twichell D, Hu C, Donahue BT, Jaap WC, Palandro D, Ciembronowicz K (2005) Strange bedfellows—a deep-water hermatypic coral reef superimposed on a drowned barrier island: southern Pulley Ridge, SW Florida platform margin. Mar Geol 214:295–307

Kahng SE, Kelley CD (2007) Vertical zonation of megabenthic taxa on a deep photosynthetic reef (50–140 m) in the Au'au Channel, Hawaii. Coral Reefs 26:679–687

Kahng SE, Maragos JE (2006) The deepest, zooxanthellate scleractinian corals in the world? Coral Reefs 25:254

Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) A review of community ecology of mesophotic coral ecosystems. Coral Reefs 29 (this issue). doi:10.1007/s00338-010-0593-6

Kraeutner PH, Bird JS, Charbonneau B, Bishop D, Hegg F (2002) Multi-angle swath bathymetry sidescan quantitative performance analysis. Oceans '02 MTS/IEEE 4:2253–2263

Leathern J, Coles BW (1993) Use of laser sources for search and survey. Underwater Intervention '93, San Diego, pp 171–186

Liddell WD, Ohlhorst SL (1988) Hard substrata community patterns, 1–120 m, north Jamaica. Palaios 3:413–423

Locker SD, Hine AC, Tedesco LP, Shinn EA (1996) Magnitude and timing of episodic sea-level rise during the last deglaciation. Geology 24:827–830

Ludwick JC, Walton WR (1957) Shelf-edge calcareous prominences in the northeastern Gulf of Mexico. Am Assoc Pet Geol Bull 41:2054–2101

Macintyre IG (2007) Demise, regeneration, and survival of some western Atlantic reefs during the Holocene transgression. In:

Aronson RB (ed) Geological approaches to coral reef ecology. Springer, New York, pp 181–200
Macintyre IG, Rützler K, Norris JN, Smith KP, Cairns SD, Bucher KE, Steneck RS (1991) An early Holocene reef in the western Atlantic: submersible investigations of a deep relic reef off the west coast of Barbados, W.I. Coral Reefs 10:167–174
Mallinson D, Hine A, Hallock P, Locker S, Shinn E, Naar D, Donahue B, Weaver D (2003) Development of small carbonate banks on the south Florida Platform margin: response to sea level and climate change. Mar Geol 199:45–63
Mazel CH, Strand MP, Lesser MP, Crosby MP, Coles B, Nevis AJ (2003) High-resolution determination of coral reef bottom cover from multispectral fluorescence laser line scan imagery. Limnol Oceanogr 48:522–534
Menza C, Kendall M, Rogers C, Miller J (2007) A deep reef in deep trouble. Cont Shelf Res 27:2224–2230
Miller JE, Vogt S, Hoeke R, Ferguson S, Appelgate B, Smith JR, Parke M (2006) Bathymetric atlas and website for the northwestern Hawaiian Islands. Atoll Res Bull 543:409–422
Montaggioni LF (2005) History of Indo-Pacific coral reef systems since the last glaciation: development patterns and controlling factors. Earth Sci Rev 71:1–75
Moore CH Jr, Graham EA, Land LS (1976) Sediment transport and dispersal across the deep fore-reef and island slope (-55 m to -305 m), Discovery Bay, Jamaica. J Sediment Petrol 46:174–187
Moore KD, Jaffe JS, Ochoa BL (2000) Development of a new underwater bathymetric laser imaging system: L-bath. J Atmos Ocean Tech 17:1106–1117
Morelock J, Schneidermann N, Bryant WR (1977) Shelf reefs, southwestern Puerto Rico. In: Frost SH, Weiss MP, Saunders JB (eds) Reefs and related carbonates—ecology and sedimentology. Studies in geology 4. Am Assoc Pet Geol, Tulsa, pp 17–25
Nemeth RS (2005) Population characteristics of a recovering U.S. Virgin Islands red hind spawning aggregation following protection. Mar Ecol Progr Ser 286:81–97
Nemeth RS, Herzlieb S, Kadison ES, Taylor M, Rothenberger P, Harold S, Toller W (2004) Coral reef monitoring in St. Croix and St. Thomas, U.S. Virgin Islands. Final report submitted to Department of Planning and Natural Resources, U.S. Virgin Islands, p 79
Nicholson JW, Healey AJ (2008) The present state of autonomous underwater vehicle (AUV) applications and technologies. Mar Tech Soc J 42:44–51
NOAA (2001) Benthic habitats of Puerto Rico and the U.S. Virgin Islands (CD-ROM). U.S. National Oceanic and Atmospheric Administration, National Ocean Service, National Centers for Coastal Ocean Science, Biogeography Program. Silver Spring, MD. Available from: http://ccma.nos.noaa.gov/ecosystems/coralreef/usvi_pr_mapping.html
Phillips NW, Gettleson DA, Spring KD (1990) Benthic biological studies of the southwest Florida Shelf. Am Zool 30:65–75
Potter JR (2008) Underwater sonar: plenty of new twists to an old tale. Mar Tech Soc J 42:68–74
Precht WF, Aronson RB, Deslarzes KJP, Robbart ML, Evans DJ, Zimmer B, Duncan L (2008) Long-term monitoring at the East and West Flower Garden Banks, 2004-2005—Interim report. Volume II: Appendices. U.S. Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, Louisiana. OCS Study MMS 2008-028, p 1330
Puglise KA, Hinderstein LM, Marr JCA, Dowgiallo MJ, Martinez FA (2009) Mesophotic coral ecosystems research strategy: international workshop to prioritize research and management needs for mesophotic coral ecosystems, Jupiter, Florida, 12–15 July 2008. NOAA Technical Memorandum NOS NCCOS 98 and OAR OER 2, Silver Spring, MD, p 24
Pyle RL (2000) Assessing undiscovered fish biodiversity on deep coral reefs using advanced self-contained diving technology. Mar Tech Soc J 34:82–91
Read JF (1985) Carbonate platform facies models. Am Assoc Pet Geol Bull 69:1–21
Rezak R, Bright TJ, McGrail DW (1985) Reefs and banks of the northwestern Gulf of Mexico. Wiley, New York, p 259
Riegl B, Piller WE (2003) Possible refugia for reefs in times of environmental stress. Int J Earth Sci 92:520–531
Riegl BM, Purkis SJ, Houk P, Cabrera G, Dodge RE (2008) Geologic setting and geomorphology of coral reefs in the Mariana Islands (Guam and the Commonwealth of the Northern Mariana Islands). In: Riegl BM, Dodge RE (eds) Coral reefs of the USA. Springer Science, Berlin, pp 691–718
Rivero-Calle S, Armstrong RA, Soto-Santiago FJ (2009) Biological and physical characteristics of a mesophotic coral reef: Black Jack reef, Vieques, Puerto Rico. Proc 11th Int Coral Reef Symp: 567–571
Rohmann SO, Hayes JJ, Newhall RC, Monaco ME, Grigg RW (2005) The area of potential shallow-water tropical and subtropical coral ecosystems in the United States. Coral Reefs 24:370–383
Rooney J, Wessel P, Hoeke R, Weiss J, Baker J, Parrish F, Fletcher C, Chojnacki J, Garcia M, Brainard R, Vroom P (2008) Geology and geomorphology of coral reefs in the Northwestern Hawaiian Islands. In: Riegl BM, Dodge RE (eds) Coral reefs of the USA. Springer Science, Berlin, pp 519–571
Rooney J, Donham E, Montgomery T, Spalding H, Parrish F, Boland R, Fenner D, Gove J, Vetter O (2010) Mesophotic coral ecosystems in the Hawaii Archipelago. Coral Reefs 29 (this issue). doi:10.1007/s00338-010-0596-3
Schmahl GP, Hickerson EL, Precht WF (2008) Biology and ecology of coral reefs and coral communities in the Flower Garden Banks region, northwestern Gulf of Mexico. In: Riegl BM, Dodge RE (eds) Coral reefs of the USA. Springer Science, Berlin, pp 221–261
Schroeder WW, Dardeauz MR, Dindo JJ, Fleischer P, Heck KL Jr., Shultz AW (1988) Geological and biological aspects of hardbottom environments on the L'MAFLA shelf, northern Gulf of Mexico. Proc Oceans '88 Conf, pp 17–21. doi: 10.1109/OCEANS.1988.23457
Seiglie GA (1971) Relationships between the distribution of *Amphistegina* and the submerged Pleistocene reefs of western Puerto Rico. Transactions of the 5th Caribbean Geological Conference. Queens College Press, New York, pp 141
Sherman C, Nemeth M, Ruíz H, Bejarano I, Appeldoorn R, Pagán F, Schärer M, Weil E (2010) Geomorphology and benthic cover of mesophotic coral ecosystems of the upper insular slope of southwest Puerto Rico. Coral Reefs 29 (this issue). doi:10.1007/s00338-010-0607-4
Singh H, Armstrong RA, Gilbes F, Eustice R, Roman C, Pizarro O, Torres J (2004) Imaging coral I: imaging coral habitats with the SeaBED AUV. Subsurf Sens Technol Appl 5:25–42
Smith TB, Blondeau J, Nemeth RS, Pittman SJ, Calnan JM, Kadison E, Gass J (2010) Benthic structure and cryptic mortality in a Caribbean mesophotic coral reef bank system, the Hind Bank Marine Conservation District, U.S. Virgin Islands. Coral Reefs 29 (this issue). doi:10.1007/s00338-009-0575-8
Strasburg DW, Jones EC, Iversen RTB (1968) Use of a small submarine for biological and oceanographic research. ICES J Mar Sci 31:410–426
Torresan ME, Gardner JV (2000) Acoustic mapping of the regional seafloor geology in and around Hawaiian ocean dredged-material disposal sites. Open-File Rep US Geol Surv 00-124
Vize PD (2006) Deepwater broadcast spawning by *Montastraea cavernosa*, *Montastraea franksi*, and *Diploria strigosa* at the Flower Garden Banks, Gulf of Mexico. Coral Reefs 25:169–171

Weaver DC, Dennis GD, Sula KJ (2002) Northeastern Gulf of Mexico coastal and marine ecosystem program: Community structure and trophic ecology of demersal fishes on the Pinnacles Reef Tract; Final synthesis report, USGS BSR-2001-0008 and MMS 2002-034, p 92

Weaver DC, Naar DF, Donahue BT (2006) Deepwater reef fishes and multibeam bathymetry of the Tortugas South Ecological Reserve, Florida Keys National Marine Sanctuary, Florida. In: Emerging technologies for reef fisheries research and management. NOAA Professional Paper NMFS (5). NOAA, Seattle, WA, pp 48–68

Zawada DG, Thompson PR, Butcher J (2008) A new towed platform for the unobtrusive surveying of benthic habitats and organisms. Rev Biol Trop 56(Suppl. 1):51–63