Coral Reefs
DOI 10.1007/s00338-015-1360-5

REPORT

Mesophotic coral ecosystems under anthropogenic stress: a case study at Ponce, Puerto Rico

Richard Appeldoorn[1] · David Ballantine[1] · Ivonne Bejarano[1] · Milton Carlo[1] · Michael Nemeth[1] · Ernesto Otero[1] · Francisco Pagan[1] · Hector Ruiz[1] · Nikolaos Schizas[1] · Clark Sherman[1] · Ernesto Weil[1]

Received: 5 February 2015 / Accepted: 24 September 2015

Abstract Mesophotic coral ecosystems (MCEs) were compared between La Parguera and Ponce, off the south coast of Puerto Rico. In contrast to La Parguera, Ponce has a narrow insular shelf and hosts several river outlets, a commercial port, a regional sewage treatment plant with associated deep water outfall, and three deep dredge disposal sites. Off Ponce, MCEs receive higher (16×) rates of sedimentation than off La Parguera, a less impacted site. The most impacted sites were located offshore of Cayo Ratones and are in or down-current and in close proximity to one of the dredge disposal sites. There, MCEs are characterized by a steep, irregular, rocky slope with a cover of fine-grained, dark brown sediment, which increases with depth. At shallower depths, scattered rocky outcroppings are colonized by sponges, black corals and algae. The sediment cover contains two to three times the terrigenous content and a significantly higher percentage of the fine-grained fraction than off La Parguera. Thirteen remotely operated vehicle (ROV) dives east and west of Ponce showed that the deepest depth at which corals were observed increased with distance from Cayo Ratones and did not approach depths observed off La Parguera except at the eastern-most (up-current) site, Caja de Muertos, which was also significantly further offshore. Benthic communities off Caja de Muertos were comparable to those at La Parguera, while off Cayo Ratones, there were no mesophotic corals and sparse development of other benthic macrobiota except sponges. Management authorities should include MCEs when assessing potential impacts from anthropogenic activities and take the necessary steps to reduce local threats.

Keywords Mesophotic coral ecosystems (MCEs) · Anthropogenic stress · Sedimentation · Benthic communities · Management · Fishes

Introduction

Mesophotic coral ecosystems (MCEs) are viewed as deeper extensions of shallow coral reefs where light levels are reduced but where photosynthesis is still important for community development (Hinderstein et al. 2010). New technologies, especially the use of mixed-gas technical diving and closed-circuit rebreathers (Sherman et al. 2009; Jessup 2014), have recently opened MCEs to a level of exploration and study previously only viable to depths up to 30 m using conventional scuba. Such work has gradually brought MCEs into focus, with studies revealing aspects of community structure and ecology (e.g., Kahng and Kelley 2007; Armstrong et al. 2009; Lesser et al. 2009; Venn et al. 2009; Kahng et al. 2010, 2014; Sherman et al. 2010; Bongaerts et al. 2011a; Olson and Gao 2013; Bejarano et al. 2014), photosynthetic adaptations (e.g., Lesser et al. 2010; Bongaerts et al. 2011b; Cooper et al. 2011) and connectivity between mesophotic and shallow communities (e.g., Slattery et al. 2011; van Oppen et al. 2011; Bejarano Rodríguez 2013; Serrano et al. 2014).

It has been generally assumed that due to their greater depth and frequently more remote locations, MCEs are less likely to be impacted by anthropogenic stress, whether from local sources (sedimentation and turbidity, invasive

Communicated by Biology Editor Dr. Mark J. A. Vermeij

✉ Richard Appeldoorn
richard.appeldoorn@upr.edu

[1] Department of Marine Sciences, University of Puerto Rico, Mayagüez 00681-9000, Puerto Rico

species, overfishing and eutrophication) or global climate change (temperature increases and associated bleaching or disease outbreaks) (Bongaerts et al. 2010; Hinderstein et al. 2010; Bridge et al. 2013). An extension of this is the deep reef refugia hypothesis (see Bongaerts et al. 2010), in which MCEs are viewed as refugia for many shallow coral reef species that potentially form the basis for reseeding degraded shallow reefs. Supporting this idea, Bak et al. (2005) found coral assemblages at 30 and 40 m to be more stable than shallow assemblages, which had shown a progressive decline in percent cover and number of species over a 30-yr period. However, their work also showed that the declines that did occur among mesophotic corals were limited primarily to shallow water species, as opposed to the agaricid corals that dominate at deeper depths. Recent work further suggests that benthic MCEs can be divided into upper and lower communities (Sherman et al. 2010; Slattery et al. 2011; Kahng et al. 2014), with the deeper MCEs characterized by more distinct species assemblages and thus not contributing significantly to any refuge function.

Bongaerts et al. (2010) conducted a thorough literature review of the deep reef refugia hypothesis by tabulating known natural and anthropogenic impacts such as storm events, disease outbreaks, algal blooms and coral bleaching. While they concluded that MCEs “have their own set of occasional stressors” (Bongaerts et al. 2010), their study was narrow in two important respects. First, of the 19 case studies examined, impacts extended into mesophotic depths in only ten cases. This may result from the natural bias that most studies were initiated to study or monitor coral reef communities in generally unimpacted areas. Second, all but two of the studies were limited to depths less than 50 m. Exceptions to these are the works of Edinger (2012), who specifically studied the impact of submarine tailings disposal at 82 m depth and its dispersal into shallower depths, and of Lesser and Slattery (2011), who documented the potential impact of invasive lionfish on benthic communities in the Caribbean down to 92 m depth.

The current study had three primary objectives. The first was generally exploratory, with the specific goal of examining MCEs at a location suspected of being under significant stress from multiple sources. The second objective was to focus on potential impacts at depths of 50 m or greater, and the third was to compare the mesophotic fish and benthic communities in these areas to local and remote less impacted sites. The exploratory work was conducted through a series of remotely operated vehicle (ROV) dives, while the detailed comparisons were based on analysis of diver-based photo-transects.

Methods

Site description

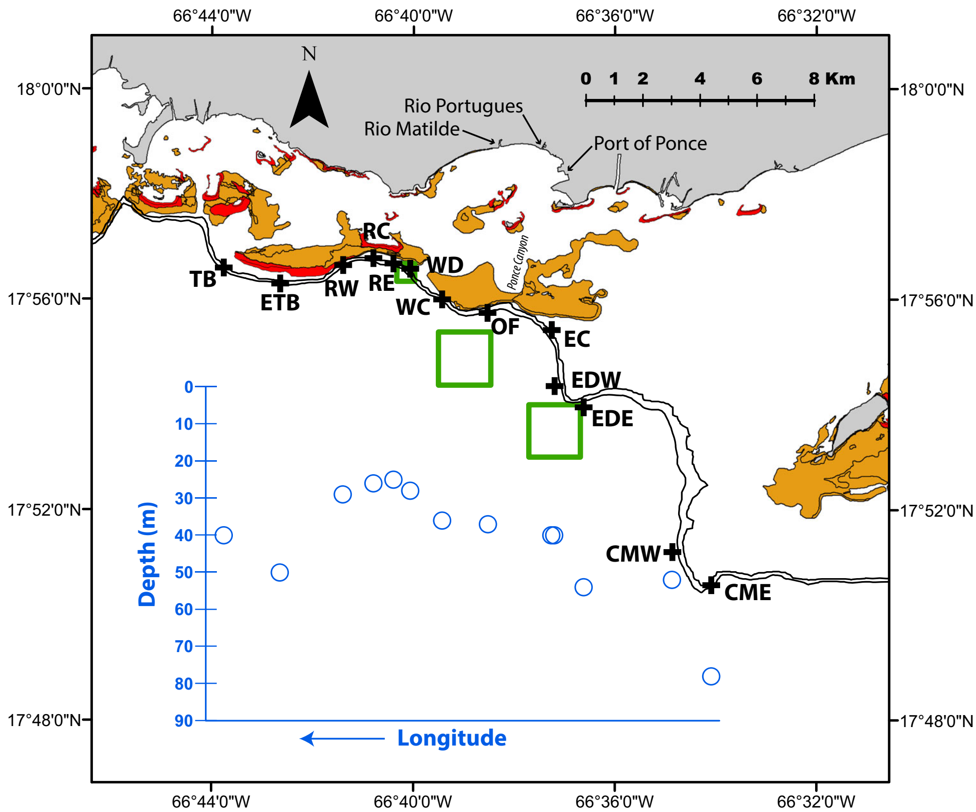
The general area studied was immediately offshore and both upstream and downstream of the city of Ponce, located on the south central coast of Puerto Rico facing the Caribbean Sea (Fig. 1). Ponce is the most populated municipality ($\sim$600,000 people) in Puerto Rico outside the San Juan metropolitan area. Potential stressors in the area are associated with the outflow of several rivers (particularly, the Rio Matilde and Rio Portugues), the Port of Ponce and its recent expansion as the Port of the Americas, and a regional sewage treatment plant with associated deep outfall. Additionally, the insular slope adjacent to Ponce is just 3–4 km from shore, rapidly expanding to 14 km from shore, upstream to the east (Fig. 1).

The sediment dynamics of the shelf in and around Ponce were described in detail by Acevedo et al. (1989). The inshore Ponce basin extends immediately off Ponce 3 km to the west. Sediments within the basin are terrigenous silts and clays, which can be resuspended by wave action and ship traffic. The resulting sediment plume is transported westward by currents and is considered a point source for sedimentary material in the region (Acevedo et al. 1989). Extending south from Ponce is the Ponce Submarine Canyon, which is covered by sediments similar to the Ponce basin although they have not been mapped out to the insular slope (Acevedo et al. 1989).

There are three deepwater dredge spoil disposal sites located off Ponce, initially developed for the Port of Ponce. In the mid-2000s, the port was expanded to accommodate post-Panamax freighters and the Ponce Harbor navigational channel and turning basin were further dredged, with approximately 5.5 million cubic meters of sediment removed. While most of the materials were deposited within the designated disposal site (the most southeastern site in Fig. 1), on a number of occasions in 2006, there were incidences of dumping short of the designated site.

The 5.6-km-long Ponce deepwater outfall was constructed in the late 1990s to accommodate the new regional sewage treatment plant. The pipe is buried as it crosses the insular platform. At the shelf edge, at a depth of 35 m, the tube runs along the surface down to a depth of 125 m. The section along the insular slope down to 70 m was backfilled with large calcareous boulders. At the end of the pipe, a series of diffusers create a broad area for mixing the effluent into the surrounding seawater. The design flow for the outfall was 1.9 $m^3 s^{-1}$. The outfall opened in October 1999 and operated under a 301 (h) waiver from the Puerto Rico Environmental Quality Board (Grace 2007). This

Fig. 1 Map of study sites off Ponce, Puerto Rico plus overlying graph of the depth of the deepest coral observed in ROV dives at each site. *Red areas* are linear reef, while *golden areas* are a mix of colonized pavement or bed rock or areas of patch reef and scattered coral rock derived from the NOAA Benthic Habitat Map for Puerto Rico. The *two black lines* are the approximate 50- and 100-m-depth contours. The *three green boxes* are dredge disposal sites. *Crosses* represent the location of the ROV dives. Location codes are given in Table 1



allows coastal communities to discharge less than secondary-treated effluent to deep ocean waters provided that such discharges meet all applicable water quality criteria and do not harm sensitive marine communities such as coral reefs and fish spawning areas. No subsequent impact assessments were carried out. In 2001, leaks were discovered at depths of 20 and 120 m (Grace 2007). The shallow leak was repaired in 2006, as were all but one of the deep leaks; in 2006, the waiver was amended to allow one deepwater leak as an additional authorized discharge point.

ROV surveys

Initial exploration of MCEs off Ponce was conducted with a Seabotix LBV200 ROV operated off a 12.8-m vessel. The ROV was equipped with a color video camera (570 lines), LED lights, parallel lasers for size estimation and a sampling arm. Video from all dives was recorded and digitized. A total of 13 sites were examined along an 18-km stretch of the coast extending east (up-current) and west (down-current) from Ponce (Fig. 1; Table 1). Sites were located along the insular slope and were selected based on local nautical charts coupled with the boat's depth recorder. Most sites were chosen based on their proximity to specific features (e.g., outfall, dredge disposal sites, shallow emergent reefs, shelf-edge promontories) subject to the constraint of spacing out observations along the stretch of coast. The ROV dives generally lasted an average of 50 min (range 22–65 min) and ranged between 72 and 111 m maximum depth depending on location (Table 1).

Benthic and fish surveys

Quantitative benthic surveys were made in November 2010 at two sites based on the ROV dives (Table 1). The two sites represented the perceived most (Ratones East) and least (Caja de Muertos East) impacted sites, with the latter used as a local control site. Diving operations followed previously established protocols for equipment, safety and dive profiles (Sherman et al. 2009) and involved a team of four technical divers using Ambient Pressure Diving Ltd./Silent Diving Systems LLC Inspiration closed-circuit rebreathers with vision electronics. Dives were made to target depths of 50 and 70 m. Upon reaching the target depth, divers would work in two teams, one focusing on conducting a continuous high-resolution benthic phototransect 10 m long by 40 cm wide (Sherman et al. 2009, 2010). The photo-transect consisted of sequential quadrat photographs, each 40 × 60 cm, taken with a 10.2 MP digital camera (Nikon D200) in an underwater housing (Titan D200) fitted with two Inon Z-240 strobes. The number of photo-quadrats per transect was variable

Table 1 Exploratory ROV dives off Ponce, Puerto Rico

Site name	Code	Location		Date	Duration (min)	Maximum dive depth	Maximum coral depth
		Latitude	Longitude				
Ponce							
Caja de Muertos East	CME	17.843	−66.568	18-Feb-10	54	102	78
Caja de Muertos West	CMW	17.853	−66.581	18-Feb-10	56	104	52
East Dumpsite East	EDE	17.899	−66.610	18-Feb-10	61	99	54
East Dumpsite West	EDW	17.906	−66.620	18-Feb-10	36	96	40
East of Channel	EC	17.924	−66.621	17-Feb-10	22	72	40
Outfall	OF	17.929	−66.642	19-Feb-10	56	98	37
West of Channel	WC	17.933	−66.657	19-Feb-10	44	85	36
West Dumpsite	WD	17.943	−66.668	17-Feb-10	56	99	28
Ratones East	RE	17.945	−66.673	17-Feb-10	55	108	25
Ratones Center	RC	17.946	−66.680	17-Feb-10	65	100	26
West of Ratones	RW	17.944	−66.690	19-Feb-10	46	95	29
East of Tallaboa	ETB	17.938	−66.711	19-Feb-10	53	111	50
Tallaboa	TB	17.943	−66.730	19-Feb-10	58	105	40
La Parguera (control)							
Hole-in-the-Wall		17.884	−67.021	30-Apr-08	36	93	87
El Hoyo		17.877	−67.041	30-Jan-08	40	101	94

Dive and coral depths are in meters. Location codes are used in Fig. 1. Comparable information is given for control sites off La Parguera

depending upon the degree of quadrat overlap, with the minimum being 17. The second team conducted visual census fish counts along two standard 15 min, 10 × 3 m belt transects (Bejarano et al. 2014). All fishes were identified to species, following Nelson (2006), and counted.

In addition to the two sites at Ponce, this analysis further included two sites located along the insular slope 11 km south of La Parguera, 44 km to the west, as distant control sites. These two sites, El Hoyo (67°2.46′W, 17°52.53′N) and Hole-in-the-Wall (67°1.33′W, 17°53.07′N), were the focus sites of detailed studies using the same methodology and represent a southeast-facing, low rugosity, shallow slope site and a southwest-facing, high rugosity, steep slope site, respectively (Sherman et al. 2009, 2010).

For each 40 × 60 cm digital photograph, percent cover was calculated by overlaying 100 random points using Coral Point Count with an Excel extension (CPCe) (Kohler and Gill 2006). To reduce clustering, each photograph was stratified into a 10 × 10 grid and one point was randomly positioned within each grid cell. Identifications associated with the random points were classified into 29 "taxa" that focused primarily on the algae and scleractinian corals as follows: corals (13 spp.); gorgonians; sponges; algae (12 taxa including cyanobacteria); sand; and pavement. These data were then analyzed to compare sites and depths. Algal identifications and nomenclature followed Taylor (1960) as updated by Ballantine and Aponte (2002) and www.algaebase.org. Scleractinian coral identification followed Wells (1973) and Humann and DeLoach (2001a) with nomenclature from www.reefbase.org, while those for the lumped invertebrate categories followed Colin (1978) and Humann and DeLoach (2001b).

All analyses were run using the PRIMER 6 statistical package (Primer-E Ltd., UK). Non-metric multidimensional scaling ordination (nMDS; Kruskal and Wish 1978), a method which uses the rank order of similarities between samples rather than their absolute values, was chosen because it has several conceptual advantages over other methods and has been shown empirically to be very robust for analyzing benthic data (Warwick et al. 1990). The ordination procedure results in a two-dimensional plot in which each transect is represented by a point and the distances between points follow the same rank order as the pairwise dissimilarities in species composition between samples. The extent to which confidence may be placed in the pattern is indicated by a "stress" coefficient. The stress coefficient is a measure of how well the configuration matches the data (Kruskal and Wish 1978), with higher coefficients indicating poorer results. A stress value below 0.20 indicates a useful two-dimensional representation with little prospect of a misleading interpretation (Kruskal and Wish 1978). A variation of the Bray–Curtis measure of dissimilarity (Bray and Curtis 1957) was applied to the square-root-transformed species coverage data (Yoshioka 2008).

Water quality and sediment characterization

Turbidity, chlorophyll *a* and temperature measurements were taken using a self-contained underwater fluorescence apparatus (SCUFA II, Turner Designs, as described in Otero 2009). The instrument was used in a moored configuration approximately 0.6 m above the bottom (50 m), and data were collected autonomously every 5–10 min. Deployment and recovery of the SCUFA unit were conducted by rebreather divers.

Characterizations of water and sediment quality were made at the two sites surveyed by divers. Instrument deployment at Ratones East was for 4 d starting 22 October 2010, but at Caja de Muertos East, the deployment was limited to 1 d due to logistical and time constraints, so most parameters were not estimated for this site. Instead, data from Ratones East were compared to similar measurements made at 50 m at the El Hoyo site. There, five deployments ranging from 7 to 12 d (54 d total) were made over the period 5 March 2009 to 27 February 2010; spaced at intervals of 2–3 months, these deployments were designed to capture seasonal variations.

Sediment samples were collected using duplicate open-mouthed containers (10 cm o.d.) installed in conjunction with the SCUFA II and covered with a 5 × 5 mm mesh to avoid the entrance of macrofauna. The traps were capped before retrieval. Sediment particles collected were used to calculate carbon and nitrogen content, $\delta^{15}N$ signature and sedimentation rates following the procedures of Otero (2009). After recovery, samples were transported to the laboratory where particles settled overnight at 4 °C. Excess water was siphoned off carefully, after which the remaining liquid with particles was transferred to centrifuge tubes and centrifuged. The resulting pellet was washed thoroughly with distilled water and dried at 60 °C to constant weight. After documenting the wet weight, samples were macerated to a fine dust using porcelain mortars and de-carbonated using 0.1 N HCl. The insoluble residue was washed thoroughly with distilled water and dried. The nitrogen stable isotope signature ($\delta^{15}N$), %N and %C were determined by inline combustion followed by infrared mass spectrometry using a Carlo Erba 1500 CHN Analyzer coupled to a Thermo-Finnigan Delta V Mass Spectrometer via a Thermo-Finnigan Conflo II Interface operated by the Stable Isotope and Soil Biology Laboratory at the Odum School of Ecology, University of Georgia. Stable isotope results are reported in ‰ using the formula $(R_{SA} - R_{ST})/R_{ST} \times 1000$ where R_{SA} is the ratio of the lighter to heavier isotope of C or N and R_{ST} is that for the standard (air was used as reference for $\delta^{15}N$).

Water samples for nutrient analysis were collected by divers using 500-mL Whirl-pak bags. Samples were transported to the laboratory and kept frozen until analysis. Samples were analyzed for nitrate and nitrite, here defined as inorganic nitrogen, and phosphates (Clesceri et al. 1998). The detection limit for inorganic nitrogen was 0.40–0.5 μM and for phosphate was up to 0.2 μM.

Additional bottom sediment samples were collected by divers at Caja de Muertos East at depths of ~55 and 66 m and at Cayo Ratones East at depths of ~50 and 55 m. Two samples were collected from each depth. In the laboratory, each sample was separated by wet sieving into a coarse/sand fraction (>63 μm) and fine/mud fraction (<63 μm), oven-dried at 60 °C and weighed (dry) to determine relative proportions of coarse versus fine material. A subsample of each was ground in an agate mortar for compositional analyses. Bulk carbon composition, including total carbon, total inorganic carbon and total organic carbon, was determined by carbon coulometry techniques (Engleman et al. 1985) conducted at the Limnological Research Center/National Lacustrine Core Facility, University of Minnesota Twin Cities. Coulometric results were converted to percent calcium carbonate, percent organic material and percent other/terrigenous material.

Results

Water quality and sediment characterization

Values characterizing the water and sediment quality observed at Ponce and La Parguera are shown in Table 2 and Fig. 2. The average chlorophyll *a* values indicate an overall higher phytoplankton biomass and productivity in waters off Ratones East (Ponce) than at El Hoyo (La Parguera); indeed, all average chlorophyll *a* concentrations at

Table 2 Water and sediment chemical characteristics from a non-impacted (Caja de Muertos East) and impacted (Ratones East) sites at Ponce compared to the control site at El Hoyo off La Parguera, Puerto Rico

Location	Water		Sediment			
	Inorganic N (μM)	Phosphates (μM)	Rate (g m^{-2} d^{-1})	C (%)	N (%)	$\delta^{15}N$ ‰ versus air
Caja de Muertos East	1.2	0.2				
Ratones East	1.1	0.3	31.7	3.5	4.5	2.8
El Hoyo	7.4	0.3	1.96	11.5	16.5	1.75

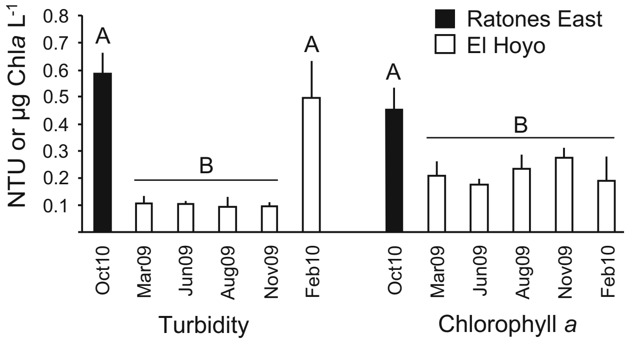


Fig. 2 Average turbidity and chlorophyll *a* concentrations measured during 7–11-d seasonal deployments off El Hoyo, La Parguera and for a single 4-d deployment off Ratones East, Ponce. *Bars* represent one SD. *Letters* represent statistical groupings determined by outlier analysis (Zar 1974) of the mean values for El Hoyo

Fig. 3 ROV video captures from the area off Ponce, Puerto Rico. ▶ **a** Caja de Muertos East at 62 m depth showing large sponges, *Antipathes* spp., black corals and an *Agaricia* sp. colony (*bottom center*). ROV grabber arm is in the *lower left corner*. **b** Caja de Muertos East at 96 m showing two colonies of the pastel soft coral (*Neospongodes portoricensis*). **c** East side of the shelf-edge promontory near the eastern disposal site at 90 m. **d** West side of the shelf-edge promontory near the eastern disposal site at 70 m. **e** Ratones East at 56 m, inside a former dredge disposal site, showing heavy siltation over reef structure. **f** Ratones Center at 90 m showing completely silted bottom. **g** Colony of *Agaricia* sp. from 50 m east of Tallaboa. Two *red spots* left of center are 5 cm apart. **h** Single photoquadrat from Ratones Center at 50 m showing a sponge, antipatharians and heavy sediment cover

El Hoyo were lower than those observed at Ratones. Similarly, average turbidity at Ratones was higher than at El Hoyo; however, during February 2010, similar turbidity values were observed at El Hoyo and Ratones. Water concentrations of phosphates were similar across sites, but approached the lower detection limits of the method. The average value for inorganic nitrogen was over six times greater at El Hoyo. However, the repeated sampling at El Hoyo shows a wide range of conditions from nutrient-poor to nutrient-rich and from well-mixed to stratified waters; thus, the significance of the differences in nutrients observed between La Parguera and Ponce cannot be determined.

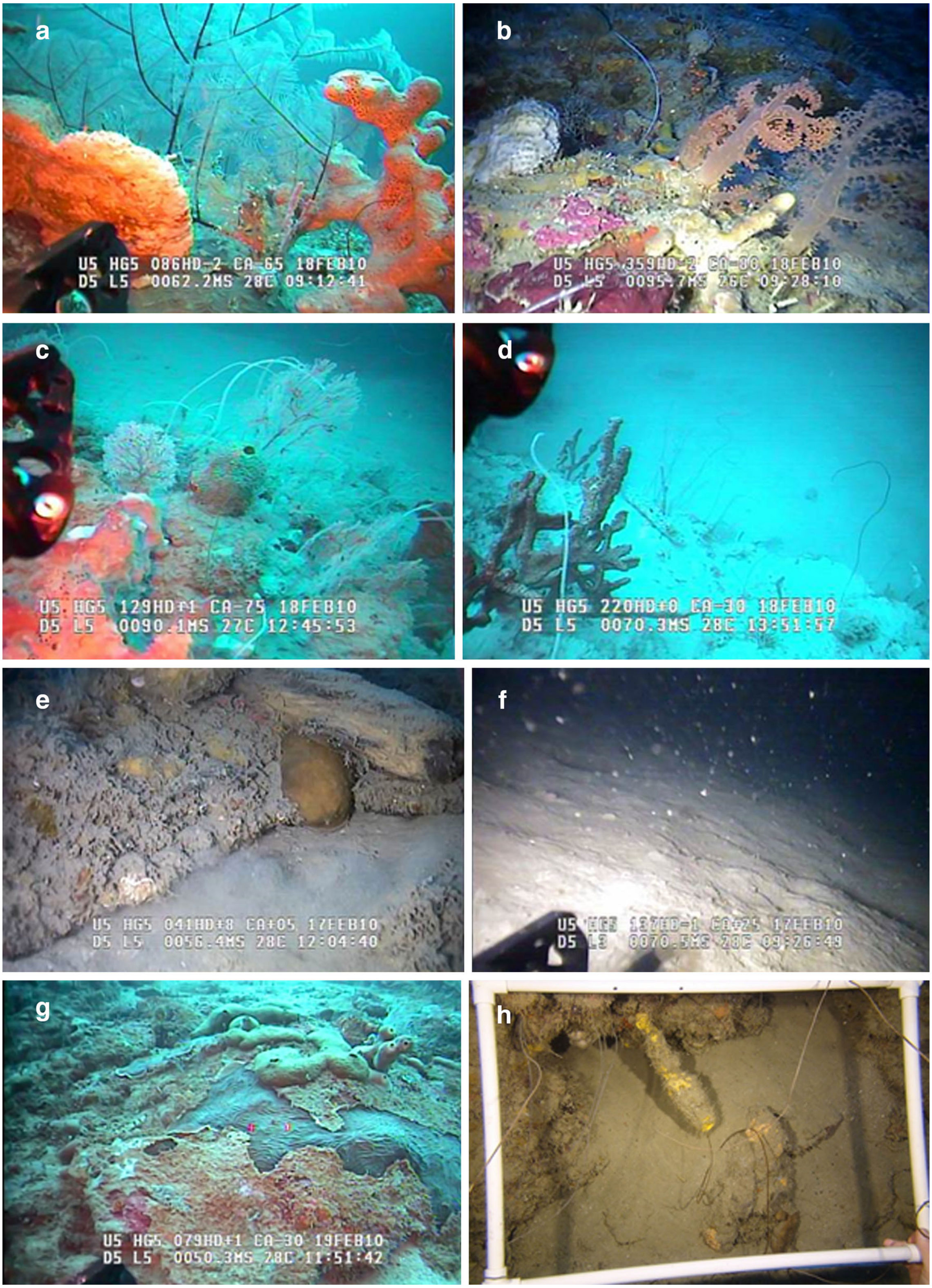
The average sedimentation rate observed at Ratones was 16 times that observed at El Hoyo. Estimation of temporal variation at Ratones was not possible, but the low standard deviation observed at El Hoyo (0.6 g m^{-2} d^{-1}) indicated a large statistical difference between the two sites. Higher sediment concentrations of C and N and lower ^{15}N content were observed at El Hoyo relative to Ratones, although the ^{15}N values at both sites were considered low. Bottom sediments from Cayo Ratones consistently contained higher amounts of fine-grained material and terrigenous material than sediments from Caja de Muertos (Table 3).

Assessment of MCEs

ROV dives showed a distinct gradient in the development of MCEs (living benthic cover, presence of corals, sedimentation, turbidity) ranging from good at the most eastern site off Caja de Muertos to very poor at sites immediately west of Ponce, especially those sites off Cayo Ratones, which were located inside or just to the west of the innermost dredge disposal site (Fig. 1). Further to the west, conditions improved but did not return to the state observed at Caja de Muertos East. Figure 3 illustrates the progression of habitat deterioration from Caja de Muertos East to Cayo Ratones. The series shows a progressive increase in the degree of sedimentation and a decline in live bottom

Table 3 Grain size and composition of bottom sediments from Ponce sites

Sample ID	Depth (m)	% Coarse (>63 µm)	% Fine (>63 µm)	% Calcium carbonate	% Organic	% Terrigenous
Caja de Muertos East						
PO-S1	55	81	19	88	1	11
PO-S2	55	92	8	94	1	5
PO-S3	66	78	22	93	1	7
PO-S4	66	85	15	92	1	7
Average		84	16	91	1	8
Ratones East						
PO-S5	55	71	29	71	2	27
PO-S6	55	60	40	65	1	34
PO-S7	50	47	53	55	2	43
PO-S8	50	43	57	51	3	47
Average		55	45	60	2	38



cover. The deeper depths off Cayo Ratones (Fig. 3f) are completely covered by dark, fine-grained sediment. At shallower depths (Fig. 3e, h), the sediment can be seen to smother parts of the original benthic cover, while some sponges are capable of clearing sediment from their tissues. Further to the west (Fig. 3g), there is some increase in

Table 4 Percent cover of benthic taxa at Ponce compared to control sites off La Parguera, Puerto Rico

	La Parguera				Ponce		
	Hole-in-the-Wall		El Hoyo		Ratones	Caja de Muertos	
	50 m	70 m	50 m	70 m	50 m	50 m	70 m
Agaricia fragilis	3.50	0.06					
Agaricia humilis	0.13	0.15	0.15	0.29			
Agaricia undata		12.74		9.71		1.40	
Agaricia grahamae		0.12					
Agaricia lamarcki	1.38					2.24	
Eusmilia fastigiata	0.22						
Madracis pharensis	0.16	2.50	0.68	1.50		0.59	
Madracis formosa	0.16						
Montastraea cavernosa	0.06		0.09	0.29			
Mycetophyllia aliciae	0.88						
Porites astreoides	0.56						
Siderastrea siderea	0.38						
Stephanocoenia intersepta	0.78	0.68	0.15	0.12			
Gorgonian				0.88	0.50	1.00	0.41
Sponge	16.66	16.00	14.65	17.94	17.50	27.70	30.10
Microdictyon boergesenii			4.88	0.76			
Halimeda spp.	0.19	0.06	0.82	4.32			
Lobophora variegata	11.31	6.97	8.68	0.88		6.71	1.06
Peyssonnelia flavescens	4.16	0.24					
Peyssonnelia gigaspora	0.00	3.85	0.00	0.32		0.76	0.00
Peyssonnelia iridescens	0.00	0.29	6.79	1.09		1.24	0.35
Peyssonnelia incomposita	0.09	0.00	0.41	0.74		0.59	0.00
Peyssonnelia sp.1	5.06	9.15	0.06	2.24		5.29	7.47
Coralline algae	11.81	18.50	3.88	16.21		14.70	20.53
Schizothrix sp.	0.22		1.00				1.06
Amphiroa spp.			2.29				
Turf	3.91	0.71	10.76	1.26	2.50	3.29	4.82
Pavement	2.50	11.53	0.21	0.94		0.35	
Sand	35.91	16.47	44.41	40.50	79.50	34.10	34.18

Values for La Parguera represent the mean of two photo-transects per site and depth, with a minimum of 17 photo-quadrats per transect

MCE development, but the habitat is still stressed, with an *Agaricia* sp. colony showing partial mortality.

This trend is mirrored in the distribution of the deepest corals (all *Agaricia* spp.) observed on each dive (Fig. 1). The deepest corals were found at Caja de Muertos East at 78 m, and the maximum depth of observed corals progressively decreased at sites toward the west. Along a 2.3-km-linear stretch of the insular slope, from West Dumpsite to the West of Cayo Ratones, no live corals were observed at mesophotic depths. Maximum depth of observed corals increased further west, indicating improving conditions, though a slight decrease was observed at the western-most site which is proximate to the oil tanker port at Tallaboa.

Detailed characterizations made by divers showed that the MCEs at Ratones East were sediment-dominated. The steep, irregular, rocky slope had a cover of fine, dark brown sediment. Scattered rocky outcroppings were colonized by sponges, black corals and algae. From depths of ~20 to ~56 m (limit of diver observations), the percent sediment cover increased with depth. The fine-grained, dark brown sediment at Ratones East was noticeably different from the buff-colored, carbonate-rich sediments characteristic of most other mesophotic sites studied in Puerto Rico. No live stony corals were noted beyond a depth of ~37 m, i.e., no corals occurred at mesophotic depths. In contrast, the habitat at Caja de Muertos East, further offshore, was more typical of other mesophotic sites studied. The outer shelf, at depths of $\sim$42 m, was an irregular hardground with a cover of algae, sponges and scattered corals. At a depth of $\sim$52 m, there is an abrupt increase in slope gradient and transition to a vertical, rocky wall. Corals, primarily agariciids, were noted to depth of at least 70 m (limit of diver observations).

Quantitative characterizations from photo-transects made at Caja de Muertos East and Ratones East (Table 4) were compared to those from La Parguera (Fig. 4). No transects were conducted at 70 m off Ratones as the whole bottom was completely covered by sediment and any disturbance resulted in resuspension and extreme reduction in visibility. The stress coefficient for the MDS ordination was 0.13, which indicates that the community patterns observed are strong. The *x*-axis of the MDS can be interpreted as degree of mesophotic benthic community development, with the Hole-in-the-Wall site off La Parguera showing the greatest benthic community development regardless of depth and Ratones East showing the least. Caja de Muertos shows a similar degree of development to the El Hoyo site off La Parguera. The latter is a low-relief, low-slope environment.

The major factor separating Ratones East from the other sites is the near-complete lack of biota. Only three live taxonomic groups were recorded (algal turf, gorgonians and sponges) with sponges accounting for 85 % of live cover. Almost 80 % of the bottom was covered by sand (Fig. 3h). At the other sites, percent cover of sand was lower, at 34–40 %, except at 70 m at Hole-in-the-Wall where it was only 16 %. The dominant benthic biota were coralline algae, the alga *Lobophora variegata* and sponges. The percent cover of sponges was similar to those seen at Ratones, except at Caja de Muertos where the cover was higher. The percent cover of coralline algae was slightly higher at Caja de Muertos and lower at 50 m at El Hoyo. At El Hoyo and Caja de Muertos, the cover of *L. variegata* was similar, while that at Hole-in-the-Wall was higher, especially at 70 m. The dominant coral was *Agaricia undata*, found at La Parguera at 70 m, but at 50 m at Caja de Muertos.

Fish composition observed during visual census at Caja de Muertos East (Table 5) showed marked differences by depth. Only a few species were distributed across the full depth range: *Halichoeres garnoti*, *Chromis insolata*, *Holocentrus rufus* and the invasive lionfish, *Pterois volitans*. Fish abundance was greater at 50 m, where a total of 14 species were observed compared to 10 species at 70 m depth. At Ratones East, the species assemblage observed at 50 m was more similar to Caja de Muertos at 70 m depth in terms of species richness and actual composition. Of the eight species observed at Ratones, half were also observed at 70 m at Caja de Muertos. Only three species were also observed at 50 m at Caja de Muertos, including *C. insolata*.

At Caja de Muertos East, average fish species richness per 30-m^2 transect (10 species at 50 m, 7 species at 70 m) was similar to that observed off of La Parguera (9.5 and 8 species, respectively; Bejarano et al. 2014). At 50 m, species composition was similar between sites, with the five most abundant species off La Parguera (*Coryphopterus personatus, Chromis insolata, Halichoeres garnoti, Clepticus parrae, Cephalopholis cruentata*) also being found at Caja de Muertos East. However, mean fish abundances per transect at Caja de Muertos East (37.5 at 50 m, 8.5 at 70 m) were both significantly lower (*t*-test, $p = 0.05$) than off La Parguera (66.6 and 32.4, respectively; Bejarano et al. 2014).

The mean species richness at 50 m off Ratones East (5.5 species) was substantially lower than observed at La Parguera or Caja de Muertos East, but the values were not significantly different due to the low sample size. In contrast, mean abundances per transect at 50 m off Ratones East (10.5) were significantly lower than at La Parguera and Caja de Muertos East (9.5) ($p = 0.05$).

Discussion

Mesophotic coral ecosystems off Ponce are clearly impacted by anthropogenic activities. Only the site farthest up-current at Caja de Muertos East showed levels of community development and depth of corals comparable to those observed off of La Parguera. The most obvious impact is associated with the western-most dredge disposal site, which extends into mesophotic depths. However, heavy sedimentation was found at least 2 km down-current from the site, suggesting that disposal occurred with substantial down-current drift, or was conducted outside the designated boundaries, or that substantial resuspension and down-current drift has occurred since initial disposal. The most recent dredging in Ponce was deposited at the most recently established, eastern-most disposal site, which is much further removed from down-current locations, but still within a few hundred meters of the insular slope. Nearby sites show higher turbidity and sedimentation compared to Caja de Muertos.

The decline in maximum coral depth closer to the Ratones and western disposal sites is a general pattern. While sites with the shallowest maximum depths of observed corals are clearly impacted by past dredge disposal, it is not possible to ascribe the sources of stress affecting the other sites. Confounding this pattern is distance from shore. Caja de Muertos East and the sites off La Parguera are situated much further offshore, and proximity

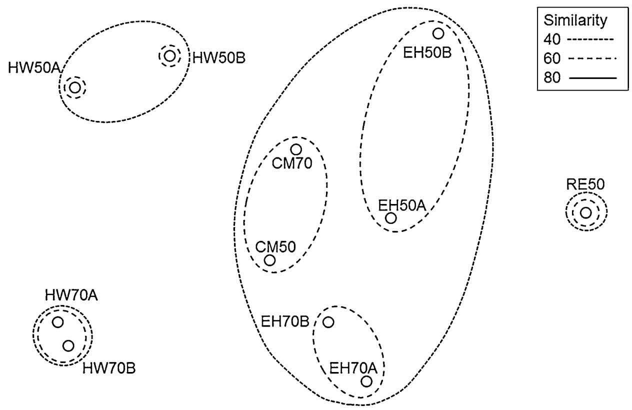


Fig. 4 Non-metric multidimensional scaling (MDS) ordination comparing benthic communities at two sites off Ponce, Caja de Muertos East (CM) and Ratones East (RE), with control sites located off La Parguera, Puerto Rico, El Hoyo (EH) and Hole-in-the-Wall (HW). Numbers are nominal depth in meters. *A* and *B* represent the two different transects quantified at each site and depth at the La Parguera sites

to shore and associated stresses due to port activities and land-based sources may play as much a role as the amount of sediment, turbidity and eutrophication affecting the general area. Thus, distance from shore may explain the large difference in short-term sedimentation rates between Ratones and La Parguera and would be consistent with the differences in bottom sediment characteristics between Cayo Ratones and Caja de Muertos. Sediment chemistry from this study, coupled with those of Otero (2009) and Otero (unpublished data), suggests that reefs toward the outer insular shelf where the shelf is wide maintain the lowest enrichment of ^{15}N, an indicator that in situ fixation of N at these locations is a predominant source of N in particles reaching shallow reefs and MCEs. While the Ratones site showed only slight evidence of ^{15}N enrichment, insufficient alone to indicate the presence of recycled or anthropogenic nitrogen reaching this reef, it did have the lowest N and C content. This is consistent with this site's proximity to Ponce and the presence of river inputs. Thus, reduced MCE development could be expected on shelf areas close to shore subjected to natural riverine inputs due to their proximity to natural sources of sediment inputs. By the same token, MCEs would be most vulnerable to further increases in stress due to elevated inputs of land-based sources of pollution.

Table 5 Fishes recorded within transects at Caja de Muertos (CDM) at 50 and 70 m and at Ratones East (RE) at 50 m off Ponce Puerto Rico

Species	Common name	CDM50		CDM70		RE50	
		1	2	1	2	1	2
Coryphopterus personatus	Masked goby	30	15				
Gramma loreto	Fairy basslet	1	3				
Scarus taeniopterus	Princess parrotfish	3					
Acanthurus bahianus	Ocean surgeonfish	2					
Thalassoma bifasciatum	Bluehead wrasse		1				
Sparisoma atomarium	Greenblotch parrotfish		1				
Gobyosoma evelynae	Sharknose goby		2				
Neoniphon marianus	Longjaw squirrelfish		1				
Clepticus parrae	Creole wrasse		1				2
Pterois volitans	Lionfish		2			1	
Cephalopholis cruentata	Graysby	2	1			1	
Halichoeres garnoti	Yellowhead wrasse	1	2	1			
Chromis insolata	Sunshinefish	1	4	1	2	1	
Holocentrus rufus	Longspine squirrelfish	1	1	1	1		
Gramma linki	Yellowcheek basslet			2	1		
Serranus phoebe	Tattler bass			1	2	1	
Myripristis jacobus	Blackbar jacobus			1			
Canthigaster rostrata	Sharpnose puffer			1			
Liopropoma mowbrayi	Cave bass			1		1	2
Lutjanus buccanella	Blackfin snapper				1	1	1
Chaetodon aculeatus	Longsnout butterflyfish				1		
Serranus tabacarius	Tobaccofish					1	
Serranus annularis	Orangeback bass					1	
	Total abundance	41	34	8	9	8	5
	Species richness	8	12	8	6	8	3

However, distance from shore alone does not indicate the extent and quality of MCE communities. In a survey of 22 sites within the US Caribbean (Sherman et al. 2013), MCEs were found throughout the region. Although well-developed sites were patchy and typically offshore, perhaps the most well-developed site was found just off the beach in the Cane Bay area of St. Croix, US Virgin Islands. Liddell et al. (1997) and Bongaerts et al. (2015) have similarly described nearshore MCEs. Off Ponce, the presence of extensive shallow shelf-edge reefs such as Cayo Ratones argues that in the distant past conditions were much more suitable for reef development, presumably including MCEs, and it is only in the more recent past that accumulated stress from coastal development, port activities, dredge disposal and watershed agriculture has degraded what were once possibly healthy ecosystems. Coring studies within MCEs may be able to unlock the historical development and decline of these systems (Hubbard et al. 2008).

The noticeable change of mesophotic benthic communities in the most impacted sites of Ponce is expected to have significant effects on the macrofauna and meiofauna of mesophotic reefs since many of these species are commensals of corals, sponges and algae. In addition, one the most important determinants of meiobenthic communities is the grain size (McIntyre 1969); therefore, the fine-grained, dark brown sediment observed in the heavily impacted sites of Ponce (e.g., Cayo Ratones) is expected to house drastically different community assemblages of meiofauna and macrofauna than those encountered in MCEs off La Parguera.

The heavy sediment coating observed at Ratones East may have contributed to lower fish abundance by reducing structural and habitat complexity. Reef complexity is consistently correlated with reef fish abundance and species richness (Gladfelter and Gladfelter 1978; Luckhurst and Luckhurst 1978; Alveizon et al. 1985; Friedlander and Parrish 1998; Syms and Jones 2000; Eagle et al. 2001), which is thought to be driven by the role of high structural complexity in reducing competition and predation (Hixon and Menge 1991; Jenkins and Sutherland 1997). In this case, however, the absence of herbivores such as surgeonfishes and parrotfishes at Ratones East may be due to the effective absence of their food base (algae). This, in turn, may be due to reduced light intensity caused by higher turbidity and phytoplankton densities relative to Caja de Muertos East. While quantitative measurements of light intensity were not made, ROV pilots reported noticeably less light at depth at Ratones East and nearby sites relative to other sites, either in Pone, La Parguera or elsewhere within the Caribbean (Sherman et al. 2013). Reduced light levels may also help explain why the fish species composition at Ratones East at 50 m more closely resembled that at 70 m at Caja de Muertos East. Light intensity has long been known to regulate the depth of many fishes, resulting in patterns of diel vertical migration (Bohl 1980; Appenzeller and Leggett 1995), typically ascribed to maintenance of optimal visual detection of prey (Townsend and Risebrow1982; Aksnes et al. 2004) but also for avoiding predators (Appenzeller and Leggett 1995). A commonly observed mesophotic predator is *Lutjanus buccanella* (blackfin snapper). Off La Parguera, this species only occurred at depths of 60 m or greater (Bejarano et al. 2014); consistent with this observation was its occurrence in one transect at 70 m at Caja de Muertos East. In contrast, the species was observed in both transects at 50 m off Ratones East.

Recent studies of MCEs (Bridge et al. 2013), especially deep MCEs (Culter et al. 2006; Bongaerts et al. 2015), have emphasized the unique species assemblages that occur at these depths. These ecosystems serve important ecological functions and provide key ecosystem services. Bejarano et al. (2014) and Bejarano Rodríguez (2013) showed that MCEs supported adult populations of commercially important fishes, acting as a refuge from intense fishing in shallow areas in some cases. MCEs also serve as nursery areas for some fishes found in shallow reefs (Brokovich et al. 2007; Bejarano Rodríguez 2013). Additionally, deep MCEs serve as important habitat for a number of threatened species, including several species of sharks (Bejarano et al. 2014) and marine turtles. Indeed, a large hawksbill turtle (*Eretmochelys imbricata*) was observed at 87 m during the ROV dive at the site east of Tallaboa. The distribution of well-developed MCEs is spatially patchy and can be related to large- and small-scale geomorphology (Sherman et al. 2010). These patches not only support a richer diversity and abundance of benthic species, but they also enhance rugosity and serve as habitat for a more abundant and diverse fish assemblage.

The potential for anthropogenic impacts in MCEs is significant, especially when areas are close to shore. Given their importance, the same management consideration given to risk assessment to shallow reefs should be extended to MCEs when evaluating potential impacts. This includes both assessment of potential impacts and subsequent monitoring of such activities as deep outfall construction and placement, dredge disposal and laying communication cables. Such consideration should also be included for coastal development projects and for projects further up in watersheds that could affect nutrient/pesticide runoff or sediment discharge associated with agriculture and urbanization, i.e., ridge-to-reef approach (Sturm et al. 2012). Recent advances in technology greatly facilitate prior and post-impact assessments of MCEs. The costs associated with technical diving, the use of small ROVs or the acquisition of high-resolution bathymetry are now compatible with other operational costs associated with large projects, and these tools can quickly map and characterize MCE communities.

Acknowledgments This work was supported by the National Oceanic and Atmospheric Administration's Center for Sponsored Coastal Ocean Research (NOAA/CSCOR) (NA06NOS4780190), through the Caribbean Coral Reef Institute. This project used the facilities of the University of Puerto Rico. We thank the captain and crew of the Orca Too for their support.

References

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

Aksnes DL, Nejstgaard J, Sædberg E, Sørnes T (2004) Optical control of fish and zooplankton populations. Limnol Oceanogr 49:233–238

Alveizon WR, Richardson R, Pitts P, Serviss G (1985) Coral zonation and patterns of community structure in Bahamian reef fishes. Bull Mar Sci 36:304–318

Appenzeller AR, Leggett WC (1995) An evaluation of light-mediated vertical migration of fish based on hydroacoustic analysis of the diel vertical movements of rainbow smelt (*Osmerus mordax*). Can J Fish Aquat Sci 52:504–511

Armstrong RA, Singh H, Rivero S, Gilbes F (2009) Monitoring coral reefs in optically-deep waters. Proc 11th Int Coral Reef Symp 1:593–597

Bak RPM, Nieuwland G, Meesters EH (2005) Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curaçao and Bonaire. Coral Reefs 24:475–479

Ballantine DL, Aponte NE (2002) A checklist of the benthic marine algae known to Puerto Rico, second revision. Constancea 83, online continuation of Univ Calif Publ Bot (1902–2002). Available at http://ucjeps.berkeley.edu/constancea/83/ballantine_aponte/checklist.html

Bejarano Rodríguez I (2013) Deep reef fishes off La Parguera insular slope, Puerto Rico, and their connectivity with shallow reefs. Ph.D. thesis, University of Puerto Rico – Mayagüez, p 115

Bejarano I, Appeldoorn RS, Nemeth M (2014) Fishes associated with mesophotic coral ecosystems in La Parguera, Puerto Rico. Coral Reefs 33:313–328

Bohl E (1980) Diel pattern of pelagic distribution and feeding in planktivorous fish. Oecologia 44:368–375

Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. Coral Reefs 29:309–327

Bongaerts P, Riginos C, Hay K, van Oppen M, Hoegh-Guldberg O, Dove S (2011a) Adaptive divergence in a scleractinian coral: physiological adaptation of *Seriatopora hystrix* to shallow and deep reef habitats. BMC Evol Biol 11:303. doi:10.1186/1471-2148/11/303

Bongaerts P, Kline DI, Hoegh-Guldberg O, Bridge TCL, Muir PR, Wallace CC, Beaman RJ (2011b) Mesophotic coral ecosystems on the walls of Coral Sea atolls. Coral Reefs 30:335

Bongaerts P, Frade PR, Hay KB, Englebert N, Latijnhouwers KRW, Bak RPM, Vermeij MJA, Hoegh-Guldberg O (2015) Deep down on a Caribbean reef: lower mesophotic depths harbor a specialized coral-endosymbiont community. Sci Rep 5:7652

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. Ecol Monogr 27:325–349

Bridge TCL, Hughes TP, Guinotte JM, Bongaerts P (2013) Call to protect all coral reefs. Nat Clim Chang 3:528–530

Brokovich E, Einbinder S, Kark S, Shashar N, Kiflawi M (2007) A deep nursery for juveniles of the zebra angelfish *Genicanthus caudovittatus*. Environ Biol Fishes 80:1–6

Clesceri LS, Greenberg AE, Eaton AD (1998) Standard methods for examination of water and wastewater. American Public Health Association, Washington, DC

Colin PI (1978) Caribbean reef invertebrates and plants. T.H.F. Publications, Inc., New Jersey

Cooper TF, Ulstrup KE, Dandan SS, Heyward AJ, Kühl M, Muirhead A, O'Leary RA, Ziersen BE, Van Oppen MJ (2011) Niche specialization of reef-building corals in the mesophotic zone: metabolic trade-offs between divergent *Symbiodinium* types. Proc R Soc Lond B Biol Sci 278:1840–1850

Culter JK, Ritchie KB, Earle SA, Guggenheim DE, Halley RB, Ciembronowicz KT, Hine AC, Jarrett BD, Locker SD, Jaap WC (2006) Pulley Reef: a deep photosynthetic coral reef on the West Florida Shelf, USA. Coral Reefs 25:228

Eagle JG, Jones G, McCormick M (2001) A multi-scale study of the relationships between habitat and the distribution and abundance patterns of the three coral reef angelfishes (Pomacanthidae). Mar Ecol Prog Ser 214:253–265

Edinger E (2012) Gold mining and submarine tailings disposal: review and case study. Oceanography 25:184–199

Engleman EE, Jackson LL, Norton DR (1985) Determination of carbonate carbon in geological materials by coulometric titration. Chem Geol 53:125–128

Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J Exp Mar Biol Ecol 224:1–30

Gladfelter WB, Gladfelter EH (1978) Fish community structure as a function of habitat structure on West Indian patch reefs. Rev Biol Trop 26:65–84

Grace RA (2007) Outfall inspections, token repairs, and major remedial works. Mar Tech Soc J 41:4–11

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 29:247–251

Hixon MA, Menge BA (1991) Species diversity: prey refuges modify the interactive effects of predation and competition. Theor Popul Biol 39:178–200

Hubbard DK, Burke RB, Gill IP, Ramirez WR, Sherman C (2008) Coral-reef geology: Puerto Rico and the US Virgin Islands. In: Riegl BM, Dodge RE (eds) Coral reefs of the USA. Springer, New York, pp 263–302

Humann P, DeLoach N (2001a) Reef coral identification: Florida Caribbean Bahamas, 2nd edn. New World Publications Inc, Jacksonville, Florida

Humann P, DeLoach N (2001b) Reef creature identification: Florida Caribbean Bahamas, 2nd edn. New World Publications Inc, Jacksonville, Florida

Jenkins G, Sutherland C (1997) The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: colonization and turnover rate of fishes associated with artificial macrophyte beds of varying physical structure. J Exp Mar Biol Ecol 218:103–125

Jessup ME (2014) Mesophotic coral ecosystems: tools and techniques for scientific exploration. In: Eckert G, Keller S, Tamone S (eds) Diving for science 2014. Proc Am Acad Underwat Sci 33rd Symp: 14–21

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

Kahng E, Copus M, Wagner D (2014) Recent advances in the ecology of mesophotic coral ecosystems (MCEs). Curr Opin Environ Sust 7:72–81

Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29:255–275

Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Comp Geosci 32:1259–1269

Kruskal JB, Wish M (1978) Multidimensional scaling. Sage Publications, Beverley Hills, California

Lesser MP, Slattery M (2011) Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. Biol Invasions 13:1855–1868

Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. J Exp Mar Biol Ecol 375:1–8

Lesser M, Slattery M, Stat M, Ojimi M, Gates R, Grottoli A (2010) Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: light, food, and genetics. Ecology 91:990–1003

Liddell WD, Avery WE, Ohlhorst SL (1997) Patterns of benthic community structure, 10–250 m, the Bahamas. Proc 8th Int Coral Reef Symp 1:437–442

Luckhurst BE, Luckhurst K (1978) Analysis of influence of substrate variables on coral reef fish communities. Mar Biol 49:317–323

McIntyre AD (1969) Ecology of marine meiobenthos. Biol Rev 44:245–288

Nelson JS (2006) Fishes of the world, 4th edn. John Wiley and Sons, Inc., New York

Olson JB, Gao X (2013) Characterizing the bacterial associates of three Caribbean sponges along a gradient from shallow to mesophotic depths. FEMS Microbiol Ecol 85:74–84

Otero E (2009) Spatial and temporal patterns of water quality indicators in reef systems of southwestern Puerto Rico. Caribb J Sci 45:68–180

Serrano X, Baums IB, O' Reilly K, Smith TB, Jones RJ, Shearer TL, Nunes FLD, Baker AC (2014) Geographic differences in vertical connectivity in the Caribbean coral *Montastraea cavernosa* despite high levels of horizontal connectivity at shallow depths. Mol Ecol 23:4226–4240

Sherman C, Appeldoorn R, Carlo M, Nemeth M, Ruiz H, Bejarano I (2009) Use of technical diving to study deep reef environments in Puerto Rico. In: Pollock NW (ed) 28th Annual AAUS Scientific Symposium, Atlanta, Georgia, American Academy of Underwater Sciences, Dauphin Island, AL, pp 58–65

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 29:347–360

Sherman C, Appeldoorn R, Ballantine D, Bejarano I, Carlo M, Kesling D, Nemeth M, Pagan F, Ruiz H, Schizas N, Weil E (2013) Exploring the mesophotic zone: diving operations and scientific highlights of three research cruises across Puerto Rico and US Virgin Islands. In: Lang MA, Sayer MDJ (eds) Proceedings of the 2013 AAUS/ESDP Curaçao Joint International Scientific Diving Symposium, October 24–27, 2013, Curaçao. American Academy of Underwater Sciences, Dauphin Island, AL, pp 297–312

Slattery M, Lesser M, Brazeau D, Stokes M, Leichter J (2011) Connectivity and stability of mesophotic coral reefs. J Exp Mar Biol Ecol 408:32–41

Sturm P, Viqueira R, Ferguson R, Moore T (2012) Addressing land based sources of pollution in Guánica, Puerto Rico. Proc 12th Int Coral Reef Symp. Available at http://www.icrs2012.com/proceedings/manuscripts/ICRS2012_21A_3.pdf

Syms C, Jones G (2000) Disturbance, habitat structure and the dynamics of a coral-reef fish community. Ecology 81:2714–2729

Taylor WR (1960) Marine algae of the eastern tropical and subtropical coast of the Americas. University of Michigan Press, Ann Arbor, Michigan

Townsend CR, Risebrow AJ (1982) The influence of light level on the functional response of a zooplanktonivorous fish. Oecologia 53:293–295

van Oppen MJH, Bongaerts P, Underwood JN, Peplow LM, Cooper TF (2011) The role of deep reefs in shallow reef recovery: an assessment of vertical connectivity in a brooding coral from west and east Australia. Mol Ecol 20:1647–1660

Venn AA, Weber FK, Loram JE, Jones RJ (2009) Deep zooxanthellate corals at the high latitude Bermuda Seamount. Coral Reefs 28:135

Warwick RM, Clarke KR, Suharsono (1990) A statistical analysis of coral community responses to the 1982–83 El Niño in the Thousand Islands, Indonesia. Coral Reefs 8:171–179

Wells JW (1973) New and old scleractinian corals from Jamaica. Bull Mar Sci 23:16–55

Yoshioka PM (2008) The Bray–Curtis similarity index remains misidentified: reply to Somerfield. Mar Ecol Prog Ser 372:307–309

Zar JH (1974) Biostatistical analysis, 4th edn. Prentice-Hall, Inc., Upper Saddle River, New Jersey