

A deep reef in deep trouble

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Abstract

The well-documented degradation of shallower reefs which are often closer to land and more vulnerable to pollution, sewage and other human-related stressors has led to the suggestion that deeper, more remote offshore reefs could possibly serve as sources of coral and fish larvae to replenish the shallower reefs. Yet, the distribution, status, and ecological roles of deep (> 30 m) Caribbean reefs are not well known. In this report, an observation of a deep reef which has undergone a recent extensive loss of coral cover is presented. In stark contrast to the typical pattern of coral loss in shallow reefs, the deeper corals were most affected. This report is the first description of such a pattern of coral loss on a deep reef. Published by Elsevier Ltd.

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1. Introduction

Most studies on Caribbean coral reefs are based on sites shallower than 30 m (e.g., see studies in Gardner et al., 2003). This concentration on shallow sites provides an incomplete and biased view of coral reefs because many reefs lie entirely or partially below this depth. Photosynthetic reefs, which have zooxanthellae and are the reef-type most studied, have a depth range that extends to at least 119 m (Reed, 1985). Their depth is limited by light penetration. Azooxanthellate reefs which are not limited by light can be found much deeper (Roberts

et al., 2006). In this report, ‘deep reefs’ refers only to photosynthetic reefs.

Shallower coral reefs have been the focus of most studies for two major reasons. First, the principal coral survey methods, basic SCUBA diving and remote sensing, are restricted to shallow waters (<30 m), due to limits of conventional diving and light penetration, respectively. Second, the survey techniques capable of penetrating to greater depths, including drop cameras, advanced SCUBA (e.g., saturation diving, mixed gas diving), remotely operated vehicles (ROVs), autonomous underwater vehicles (AUVs) and submersibles, are expensive and logistically demanding. The costs of these emerging technologies have resulted in a small fraction of studies at deep sites. Information on coral reef systems below 30 m, including where they

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are found, their ecological roles, threats to them, and their status remains poorly understood.

The few studies of deep Caribbean reefs indicate that they may be different from shallow ones. Mapping surveys show deep reefs typically have greater coral cover and lower coral diversity (Jarrett et al., 2005; Armstrong et al., 2006) and monitoring studies have not detected coral declines (Bak and Nieuwland, 1995; Bak et al., 2005) observed among shallow coral systems throughout the Caribbean (Gardner et al., 2003). Such patterns have led to the suggestion that corals on deep reefs could serve as a source of future recruits for shallow reefs during times of stress (Glynn, 1996; Riegl and Piller, 2003). Considering the paucity of data on deep reefs, there is a critical need to map and monitor their condition and investigate possible ecological linkages with shallow reefs. What if the worldwide deterioration of shallower reef systems is already affecting deeper reefs? The answer to this question is becoming more important as coastal populations continue to grow (Hoegh-Guldberg, 1999), global warming continues, and a search for ways to mitigate the decline of shallow reefs remains.

As part of a broader project to map the deep benthic habitats of the US Virgin Islands, an extensive coral mortality event was discovered on a deep reef (depth 40 m). The event was particularly noteworthy in that it was the deeper parts of the reef that were affected; a pattern inverse to that observed in studies on shallow reefs. The extent and pattern of coral mortality and lack of data for deep reefs compelled an account of these observations. In this report the mortality event is described and possible causes are discussed. The goal of this manuscript is to highlight the need for further discussion and surveys of deep reefs, and to show that deep reefs cannot be viewed as categorically invulnerable.

2. Materials and methods

In February 2005, the NOAA ship *Nancy Foster* collected video and still camera images of the seafloor around the US Virgin Islands using a Spectrum Phantom S2 remotely operated vehicle (ROV). The ROV data were collected to ground truth multibeam sonar surveys of the area. One of the mission's exploration targets was a reef, hereafter referred to as Mid-shelf reef #1 (MSR-1), situated among a network of mid-shelf reefs between the island of St. John and the insular shelf edge which is 20 km to the south (18.25°N,

64.77°W) (Fig. 1). The shallowest parts of most near-shore, mid-shelf reefs have been surveyed and described by others including Monaco et al. (2007).

MSR-1 is relatively deep, 30–40 m, and remote. A vast expanse of sand and rhodoliths extends in all directions for a minimum of 5 km. The closest developed area is the town of Cruz Bay (population 3000) on St. John, 8 km to the north. Over half of St. John and much of the surrounding water are within the Virgin Islands National Park. In general, anthropogenic impacts such as pollution and runoff are dramatically less on St. John than on many other Caribbean islands.

The ROV traversed MSR-1 from SE to NW approximately 1 m above the seafloor during daylight hours. Bathymetric survey data (source: National Oceanic and Atmospheric Administration, Satellite and Information Service) were used to direct the ROV along MSR-1's shortest cross-section. This was done to obtain imagery of all the transitions among bottom features (e.g., reef to rhodoliths, reef to sand), along the reef in the shortest amount of time. The transect represented a 1200 m × 1 m swath of MSR-1.

Video was continuously collected along the transect using a forward pointing camera to assist in visualizing three-dimensional benthic structure and to help navigate the ROV. High-resolution still images of the seafloor were systematically collected every 30 s using a downward pointing camera. The speed of the ROV was kept between 0.5 and 1 m s⁻¹ which resulted in images spaced approximately every 16 m (S.E. 1.7). Each image was estimated to cover 1 m² area ± 50 cm. An ultra-short baseline system and differential geographic positioning system were used to determine the geographic location of each image within ~5 m. A pressure sensor mounted on the ROV was used to determine the depth.

High-resolution still images (a total of 69) were used to characterize the spatial distribution of benthic cover types. For each image, the relative area of live coral, dead coral with algal turf (DCA), fleshy macroalgae, other biological cover types (e.g., sponges, coralline algae) and bare substrate was estimated visually with the aid of a 10 × 10 grid superimposed on each image.

Following analysis of the images, the transect was divided into six broad-scale reef zones based on macroscale reef morphology (Fig. 2). Zone divisions were positioned at points of inflexion in depth and divided reef valleys from ridges. Zone A, where the transect began and which was the farthest offshore

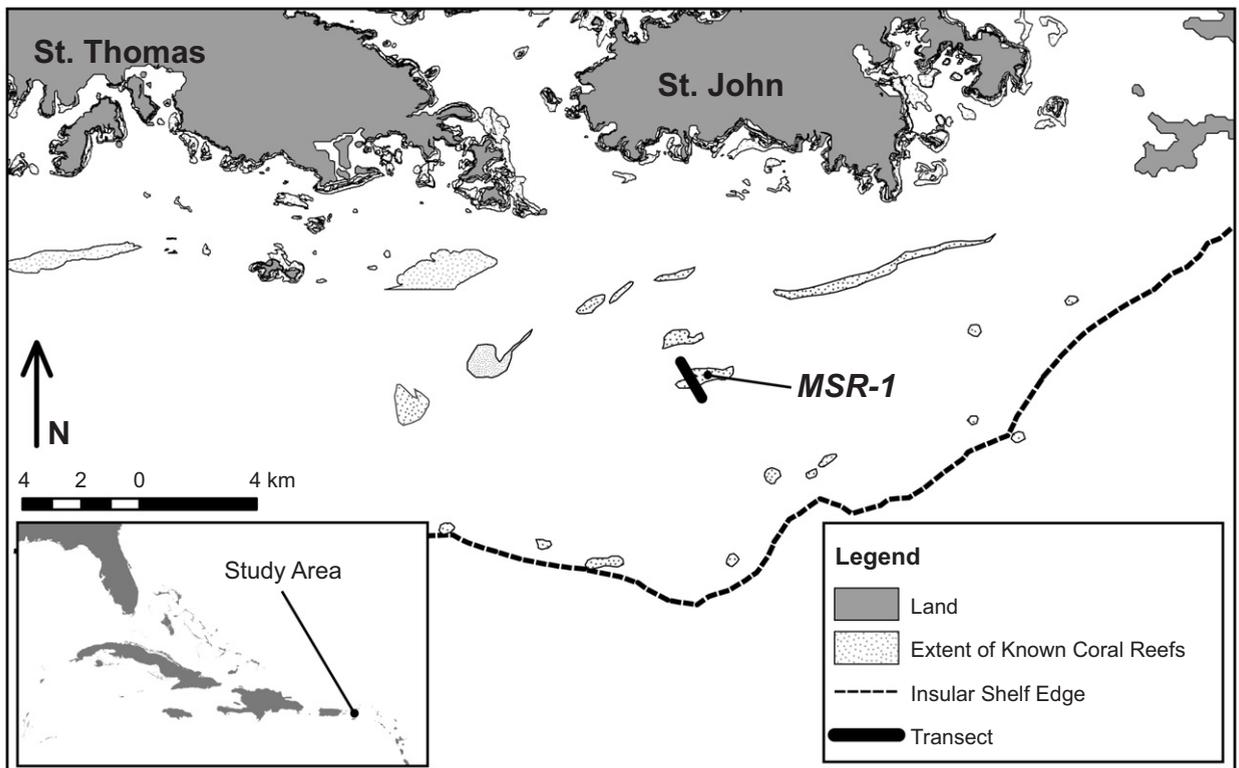


Fig. 1. Geographic location of MSR-1 and survey transect with respect to the US Virgin Islands and shelf edge. Shelf edge represented by the 100 m isobath.

zone, was a reef flat facing the insular shelf edge at a depth of 39 m. Zone B was a section of reef composed of two ridges with depths of 32 and 34 m, respectively. Zone C was a small reef valley which reached a depth similar to zone A. Zone D was a second section of reef with a ridge cresting at 35 m. Zone E was a descending section to the reef ridge in zone D and terminated at the inshore limit of MSR-1.

3. Results

The MSR-1 had an average live coral cover over the entire transect of 37.8% (SE = 4.9), with maximum cover of 80% in some areas. The highest amounts of live coral were seen in zones B and D, the shallowest parts of the transect.

The principal reef-building coral species belonged to the *Montastraea annularis* complex (composed of *M. annularis*, *M. faveolata* and *M. franksi*). The summation of cover for other coral species such as *Montastraea cavernosa*, *Agaricia lamarki*, and *Siderastrea siderea* made up less than 5% of the total

live coral cover. *Montastraea* colonies formed discrete horizontal plates, where distinct colonies overlapped each other vertically, creating a complex three-dimensional structure with high rugosity (Grauss and Mcintyre, 1982). Similar coral structure and cover was identified at shelf-edge reefs by Armstrong et al. (2006) south of St. Thomas and Clavijo and Tobias (1985) south of Puerto Rico.

Although the amount of coral cover on the MSR-1 transect was relatively high relative to the Caribbean average of 5–10% (Gardner et al., 2003), a high amount of DCA in zones A and C suggested a recent coral mortality event restricted to those deeper zones occurred (Table 1). All areas characterized as DCA were distinguished by a thin, monotone veneer of light-green filamentous algae on the surface of white coral skeleton (Fig. 3). The veneer was semi-transparent and allowed many of the underlying dead corals to be identified to the species level according to their macroscopic skeletal structure. Several times, the ROV came within 50 cm of dead coral colonies and individual intact corallites underneath the turf algae were observed. No erosion of the plate-structure or corallites was visible in these dead

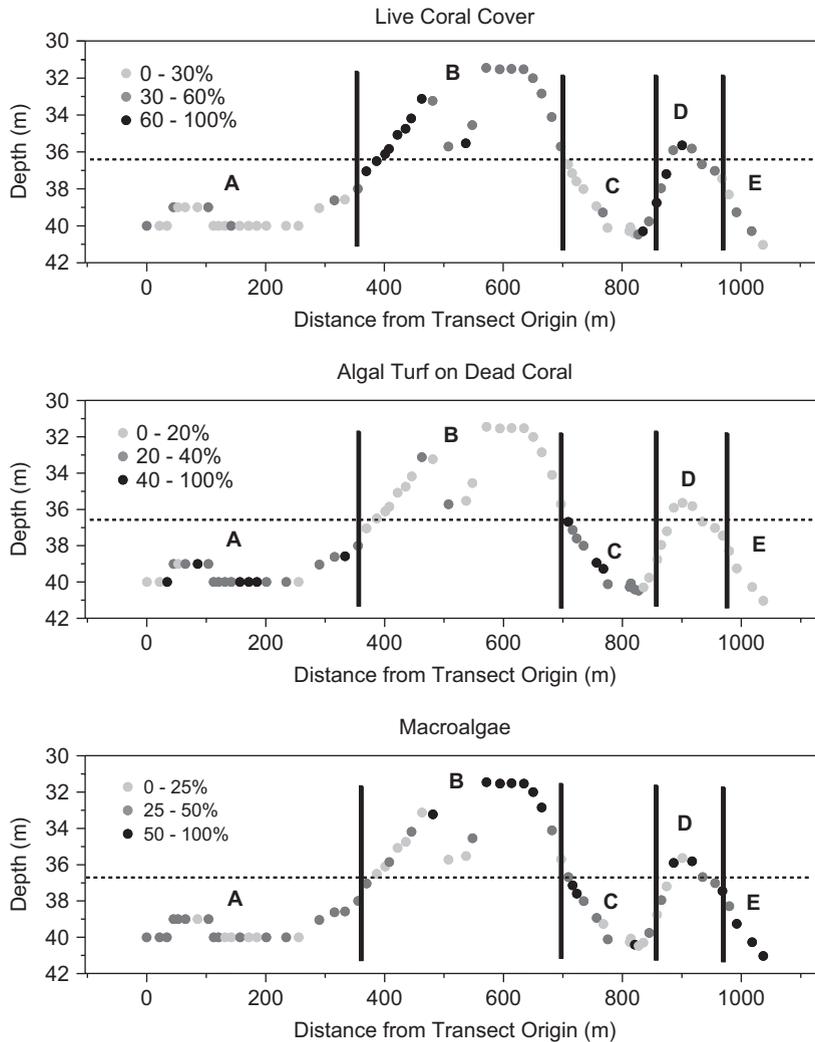


Fig. 2. Percent cover of live coral (top), dead coral with algal turf (middle) and macroalgae (bottom) along the depth profile of MSR-1. Percent cover for each chart is divided among three equiprobable classes. Letters and associated vertical breaks correspond to transect segments (A, B, C, D, and E) differentiated by macroscale reef morphology.

Table 1
Mean percentage and standard error of benthic cover types among five transect segments (A, B, C, D, and E)

Segment	n	Depth (m)	Live coral		DCA		Macroalgae		Other		Bare	
			Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
A	23	39.4	19.5	3.0	26.7	2.3	25.7	1.7	21.3	3.5	6.7	4.3
B	22	34.4	50.9	4.7	8.1	2.5	33.4	3.5	7.4	1.8	0.2	0.7
C	13	39.3	35.1	7.4	20.4	4.7	25.8	4.0	15.7	2.6	3.1	2.7
D	4	36.0	57.5	11.1	0.0	0.0	37.5	9.5	5.0	2.9	0.0	0.0
E	6	38.9	30.3	7.4	1.8	1.6	48.3	4.2	11.2	2.3	8.3	7.9

Average depth and no. of images (n) assessed in each segment are shown. DCA: dead coral with algal turf.

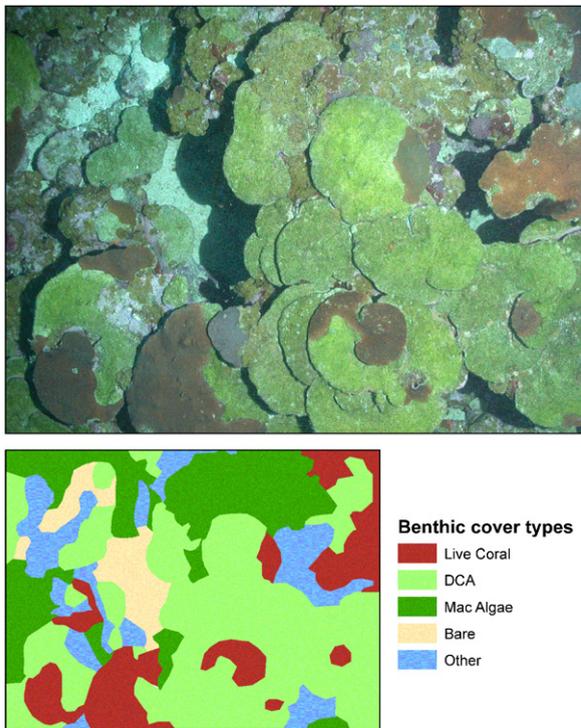


Fig. 3. An image taken on MSR-1 and the corresponding classification of benthic habitat used in cover type comparisons.

colonies covered by turf. Colonies exhibiting partial mortality had clear separation of dead (DCA cover) versus live portions of individual colonies.

Dead corals (partial or complete colony) were also colonized by fleshy macroalgae (e.g., *Dictyota* sp. and *Lobophora variegata*). Areas covered in macroalgae were clearly separated and distinct from those characterized as DCA. There are no published studies of algal succession at this depth, but shallow reef studies (e.g., McClanahan, 1997; Diaz-Pulido and McCook, 2002) suggest areas of MSR-1 covered in macroalgae are likely a later stage of algal succession than turf algae. Bare bleached coral was not observed.

Taken together, these observations suggest that the large areas of DCA with similarly thin algal colonization and little skeletal breakdown indicate that the underlying coral died as a result of a relatively recent (1 year or less) and simultaneous event in contrast to those dead corals colonized by fleshy macroalgae. No specific timeline of mortality and subsequent algal succession can be established due to a lack of studies examining coral death and algal succession rates at these depths.

Clear associations between DCA and depth, and DCA and live coral were observed. DCA was predominantly found below 36.5 m. It was found only in 2 of the 22 images shallower than this depth (Fig. 2) and almost exclusively in zones A and C, 2 of the 3 deepest areas of MSR-1. Zone E, the remaining deep area, did not possess any DCA and exhibited a different benthic composition than other zones. When compared to the average of all images collected on MSR-1, zone E possessed lower than average live coral cover and higher than average macroalgae cover. Throughout all images live coral cover and DCA were negatively correlated (Spearman; $r = -0.67$, $p < 0.001$). This negative correlation is intuitive since a gain in DCA is necessarily a loss in live coral.

Coral cover prior to the mortality event, as represented by the sum of live coral and DCA, was estimated to be 50.1%. The estimated decreases in coral cover for each segment are presented in Fig. 4. Over the entire transect, loss of coral cover was estimated to be 25%. Segments A and C, where DCA was highest, had estimated losses of 58% and 37%, respectively. Change in coral cover in zone D was 0% (no DCA observed) and in zones B and E was <20%.

The magnitude of this mortality event cannot be accurately inferred for the region or MSR-1 based on a single transect. Nonetheless, the area affected on MSR-1 was large (~500 × 1 m swath) and represented approximately 50% of the transect.

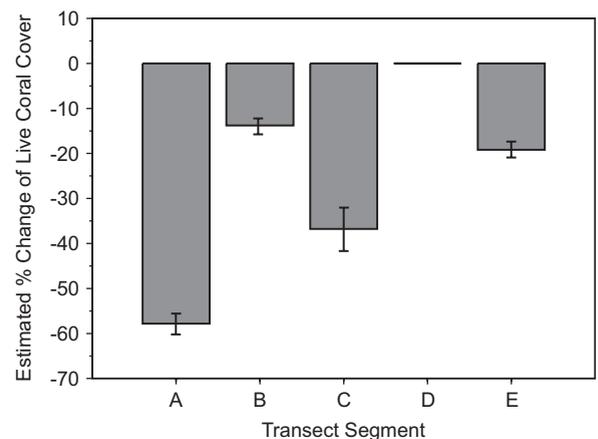


Fig. 4. Estimated mean percent change and standard error of live coral among transect segments from before and after the considered mortality event. Live coral cover from before the event was represented by the sum of live coral cover and dead coral cover with algal turf.

4. Discussion

The incidence of coral loss among the deepest sections of the transect was in stark contrast to surveys in shallow systems where coral loss is greatest in shallower corals. In shallow systems, the principal coral stressors include warm water, hurricanes, fishing, pollution and sedimentation (e.g., Glynn, 1996; Hughes and Connell, 1999; Gardner et al., 2003) the effects of which are usually limited to the upper layers of the water column. The observed coral loss which was restricted to only the deepest portions of the transect suggests that other mechanisms were involved.

Possible mechanisms for massive coral loss at deep reefs are cold-water intrusion, descended dense water masses, catastrophic sedimentation, infectious disease or some combination of these. Leichter et al. (1996) and later Leichter and Genovese (2006) showed that vertical oscillations in the thermocline caused by internal waves can transport cool deep water from the shelf edge onto the reef slope. Cool water has been shown to cause severe coral bleaching and mortality (Coles and Fadlallah, 1991; Gates et al., 1992; Glynn, 1993). Coral mortality can also be produced by warm or cold water at the sea surface descending to the seafloor (Dennis and Wicklund, 1994). Although warm water typically floats on top of higher density cool water, increased salinity caused by evaporation or wind-driven downwelling can cause a warm water mass to sink (Smith, 2001). Cold dense saline plumes caused by surface cooling can sink and spread laterally for tens of kilometers from their source (Hickey et al., 2000). In either case, if the plume comes into contact with a reef and ambient water temperature is outside the limits of coral temperature tolerance then stress, bleaching and ultimately coral death can ensue (Glynn, 1996). Catastrophic sedimentation occurs when entrained fine sediment from a storm or runoff event drops out of the water column smothering or burying corals (Bak et al., 2005). Infectious coral diseases such as Plague Type II or black band disease are caused by pathogens and can infect corals ultimately leading to coral mortality (Glynn, 1996).

The type of data collected at MSR-1 and the absence of prior data on corals or environmental variables at the survey site complicates any deduction of a cause. However, there are several details that provide some insight into plausible causes of coral loss. First, DCA along the length of the

transect was not ubiquitous. The vast majority of DCA was found at sites deeper than 37m. This observation suggests that a stratified water body or light attenuation was likely involved. Second, different coral colonies in the same image did not show homogenous patterns of coral loss; no mortality, partial mortality and complete mortality were observed. These patterns have been observed during coral bleaching from warm water or disease in shallow reefs (Miller et al., 2003; Glynn, 1996). Third, the margin between live coral and DCA (dead coral) was sharp. We have observed the same pattern on corals in shallower water that have suffered partial mortality from disease. Miller et al. (2003) observed coral mortality of *M. annularis* colonies caused by White Plague Type II at Tektite Reef, St. John. The signs of this disease are conspicuous patches of white necrotic tissue, which within 1 month are quickly covered by turf algae. Although these signs are similar to the observations described here, no signs of active coral disease were observed in the imagery and why loss from disease would be restricted to depths below 37m is not clear. Fourth, although there is a general increase of DCA found at deeper sites, the deep sites in zone E did not have DCA. This may have been caused by an onshore-offshore gradient in the mechanism involved and/or an earlier loss of coral in zone E. Intruded cold water from offshore could cause such an affect. Finally, 20 transects located on 8 other similar mid-shelf reefs in the region and surveyed in the same month did not show a corresponding abundance of DCA. These results imply the observed coral loss was a localized event. Together, the observations of coral loss on the transect point towards multiple causal factors, such as a localized disease outbreak in concert with a stratified water body which limited disease dispersion.

There is a possibility that areas of DCA will eventually be covered by living coral, but studies of coral-algae interactions in shallow reefs (Diaz-Pulido and McCook, 2002) indicates coral covered by algae are unlikely to succeed in recolonizing the area. There are no published studies which have examined coral-algal dynamics at this depth. A future survey is needed to assess the study site.

5. Conclusions

There is an impression that deep reefs such as MSR-1 could serve as refugia for corals during times of environmental stress and degradation in

shallow reefs (Glynn, 1996; Riegl and Piller, 2003). The coral loss at MSR-1 should serve as an example that deep reefs cannot be considered invulnerable and can undergo massive shifts in benthic cover similar to those widely studied in shallower systems. Additional surveys and long-term monitoring of deep reefs are needed to determine the frequency and extent of mortality events such as the one observed on MSR-1 and to assess if recovery is possible.

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