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ZONATION OF A LAGOONAL PATCH REEF: ANALYSIS, COMPARISON, AND IMPLICATIONS FOR FOSSIL BIOHERMAL ASSEMBLAGES

Rena Mae Bonem
Department of Geology
Hope College
Holland, Michigan 49423

and

George D. Stanley, Jr.
Department of Geology
University of Kansas
Lawrence, Kansas 66045

ABSTRACT

Examination of a patch reef in the backreef lagoon at Discovery Bay, Jamaica, resulted in recognition of five biotic assemblages: 1) a Porites Zone, which is dominated by sea urchins, sponges, and the finger coral, Porites; 2) a Mixed Sponge Zone, which contains algae, corals, and bivalves, but which is dominated by a variety of sponges; 3) a Madracis Zone, which is dominated almost exclusively by Madracis mirabilis; 4) a Massive Coral Zone, which contains the star coral, Montastrea, and the plate corals, Agaricia and Mycetophyllia; and 5) an Agaricia Zone of Agaricia lamarcki. The patch reef is developed on a carbonate mud bank and is surrounded by a deep water zone containing only antipatharian corals and a few mounds of burrowing organisms.

The zones were mapped and described both quantitatively and qualitatively. The biotic zonation of the patch reef clearly demonstrates distributional patterns based on response to turbidity, light penetration, salinity, water circulation, and substrate slope and composition. Anomalous occurrences of corals at shallower depths than normally expected on the fringing-barrier reef can be explained by the turbid, low light environment of the patch reef. The patch reef at Discovery Bay can provide a useful model for interpretation of those fossil reefs and bioherms interpreted as having developed on a carbonate mud substrate.

KEY WORDS: Patch Reef, Lagoon, Turbid, Zonation, Carbonate Mud, Jamaica

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RENA MAE BONEM AND GEORGE D. STANLEY, JR.

Introduction

During the past twenty years, numerous investigations have been conducted in an attempt to compare modern reefs with ancient carbonate build-ups. Although many Paleozoic and Mesozoic bioherms are associated with carbonate mud accumulation, most modern reefs are developed in clean carbonate sand. We examined a small patch reef situated in the backreef lagoon at Discovery Bay, Jamaica, in order to determine the possible influence of a mud substrate on the development of reef associations. The composition, ecology, and zonation of the Jamaican fringing-barrier reef is well known (1, 2); however, less is known about the lagoonal backreef settings. The patch reef was selected for study because it contains a well-developed association of corals and sponges in a turbid environment characterized by a carbonate mud substrate. The organisms of the patch reef occur through a depth range of 6 to 25 meters.

The following discussion includes a brief description of the composition and spatial distribution of the benthic organisms composing the patch reef, as well as possible environmental parameters responsible for the distributions. In addition, comparisons are made with patch reefs in the geologic record that may have formed under similar conditions.

Location and Setting

The patch reef investigated in this paper is referred to as the Red Buoy Patch Reef and is located in the northeast part of Discovery Bay on the north coast of Jamaica. The Red Buoy Reef is situated on a long, narrow bank that extends southwest into Discovery Bay from the shore (figure 1). The origin of this bank is not known, although it may be related to relict drainage or Pleistocene topography. Small subaqueous brackish water springs emanate from this bank (3). The patch reef biota is dominated by corals and sponges and extends from a depth of approximately 6 to 25 meters where the bottom becomes a gently sloping mud floor, interrupted only by mounds of burrowing organisms.

The substrate of the Red Buoy Patch Reef is composed of carbonate mud with varying amounts of skeletal debris. There is a large amount of suspended material in the water, which greatly reduces the light penetration. Visibility during the period of study ranged from a maximum of 5 meters to a minimum of 15 centimeters.

Method

A detailed bathymetric map of the study area was prepared as a base on which to outline the distribution of organisms. The map was constructed by taking depth readings at 160 points using standard SCUBA equipment. Points were located by using oil-filled compasses, oil-filled bourdon tube and capillary depth gauges, and a 60-meter line fixed at the base of the permanent red channel marker. The map covers an area of approximately 8000 square meters and has a 3-meter contour interval.

Once the bathymetric map was completed, the biota of the patch reef were mapped as a series of zones characterized by distinct associations of organisms (figure 1). The zones were first recognized qualitatively and later described quantitatively from two transect lines staked down underwater in various positions across the reef (figure 1, T1 and T2). The biota along the transect lines were thus described by a combination of qualitative and quantitative techniques. At each meter interval along the the line, the biota were noted with the sediment type. At every third meter, a chain 1.67 meters long (130 links) was laid perpendicular to the line. Following methods of Porter (4), the percentage of cover represented by each organism or plant beneath the chain was estimated by counting the number of links. This gave a rough estimate of the percentage of cover (figure 3). We recognize a number of problems inherent in this method: 1) patchy distribution of large colonial organisms may be deemphasized, especially if the individuals are wider than the length of the chain as is the case with some massive corals, 2) infaunal organisms were not counted, 3) evasive or vagile benthos could alter their repose with respect to the chain (anemones and sea urchins). Also, during our study, damsel fish were observed to remove the chain when it was dropped across their territories. In spite of inherent problems, we feel that our methods of analysis are valid in deliniating and describing the general character of the biotic zones.

General Description of Biotic Zones

Porites Zone

This zone covers 25 percent of the mapped area on the shallow top and sides of the bank (figure 1). This area is generally flat-lying. The zone is covered with rubble and debris of the finger coral, *Porites*. The dominant species on the two transect lines are *Haliclona rubens* (21.3%) and *Diadema antillarium* (38.9%), followed by *Porites astreoides* (11.1%). Although most of the algal encrusted rubble of this zone is dead

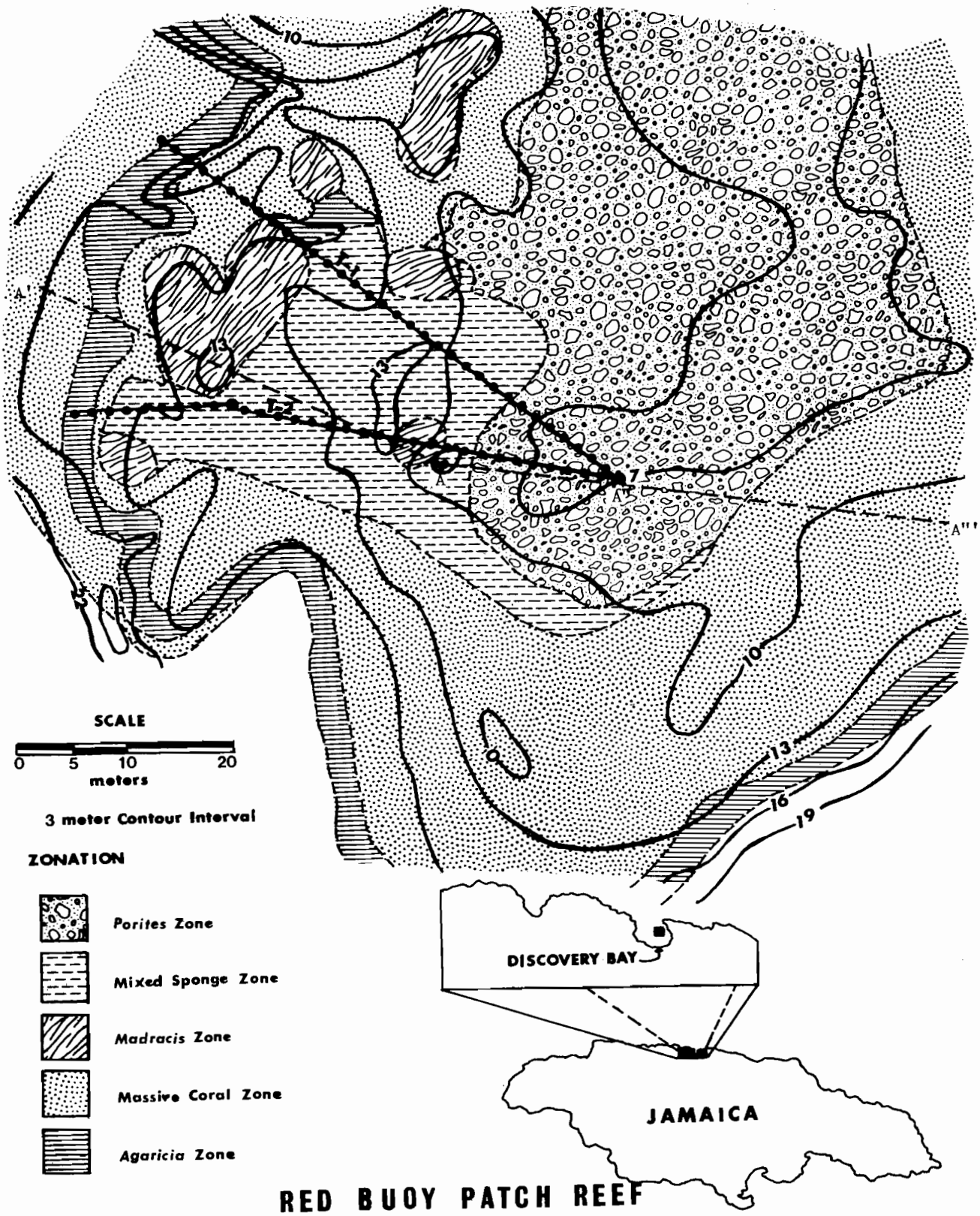

Figure 1. Zonal-bathymetric map of the Red Buoy Patch Reef. Dotted lines T1 and T2 show transect lines. Dashed lines along A, A', A", and A"' follow line of cross-sections in figure 2.

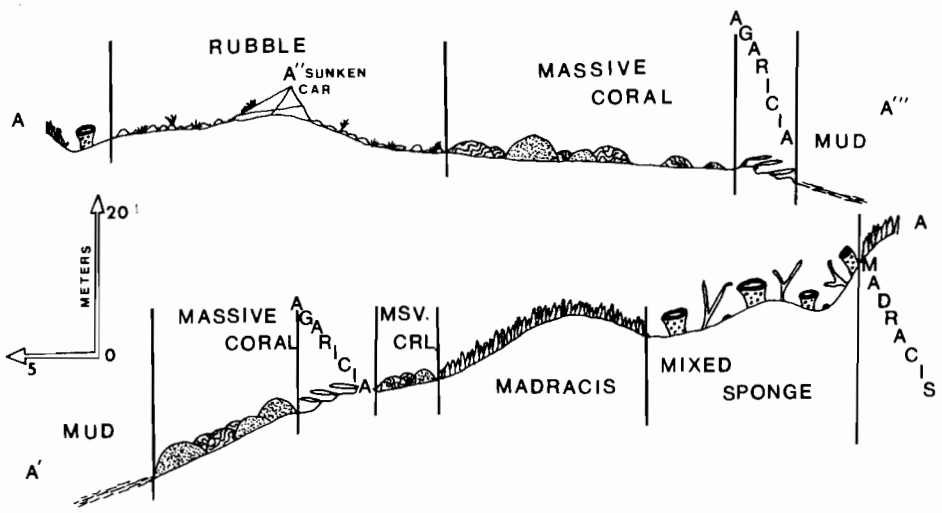

Figure 2. Cross-sectional profiles across the Red Buoy Patch Reef with zones illustrated. Refer to figure 1 for location of sections.

branches of *Porites porites*, that coral forms only 1.7 percent of the living organisms in the zone. The *Porites* Zone is the shallowest zone at the Red Buoy, ranging from 4.5 to 9 meters, with the best circulation, the greatest light penetration, and the least amount of suspended material. The hydrozoan *Millepora* occurs commonly in this zone.

Mixed Sponge Zone

The Mixed Sponge Zone is dominated by large vase, frond-like, and branching sponges. It comprises approximately 10 percent of the mapped area on the Red Buoy Reef. The most common sponges include *Haliclona dora*(8.8%) and *H. rubens* (3.9%). The zone is one of the most variable and diverse with 27 taxa including 11 sponge species (figure 3). The red alga, *Ceramium nitens* , is found in greatest numbers (28.0%), followed by the bivalve *Isognommon alatus* (7.6%), the flower coral *Eusmilia fastigiata* (6.4%), a soft encrusting coral *Erythropodium* sp. (6.6%), and *Porites astreoides* (4.2%). Although the individual sponge species occur in only small percentages, together the sponges comprise a dominant component of the zone.

Madracis Zone

This zone is dominated by the branching coral, *Madracis mirabilis* (86.6%). Other organisms include a few sponges and boring worms. The presence of the worms was noted, but not used in percentage cover calculated for the zone. The *Madracis* Zone covers less than 10 percent of the mapped area and is quite patchy in distribution (figure 1) consisting of mounds rising up to 4.5 meters, and forming conspicuous hill-like features. Numerous brackish water springs are located in and around the *Madracis* mounds. Boundaries of this zone are sharp compared to those of other zones.

Massive Coral Zone

The Massive Coral Zone has the greatest areal extent of any of the zones. It forms a broad band that commonly conforms well to the map contours (figure 1) and it covers 40 percent of the patch reef. Corals most characteristic of this zone are *Agaricia agaricites* (17.8%), and *Montastrea cavernosa* (5.8%). Also present are *Siderastrea siderea*, *Madracis mirabilis*, *Helioseris*, *Mycetophyllia*, *Manicina*, *Scolymia*, and *Porites porites*. The bivalve *Isognommon alatus* constitutes 12.5 percent of the biota. Many of the elements of this zone are large or massive, such as *M. cavernosa* and are patchy in distribution, making quantitative description difficult. The boundaries of this zone are not distinct, but merge with those of the Mixed Sponge and *Agaricia* Zones (discussed below), making definition difficult.

Agaricia Zone

The *Agaricia* Zone forms a narrow belt adjacent to the Massive Coral Zone and constitutes less than 10 percent of the mapped area. The zone is recognized by the dominance of the large, platy, shingle-like coral, *Agaricia lamarcki* (32.8%). This zone occupies a depth range of 10 to 20 meters. Other important species include *Montastrea cavernosa* (16.3%), *M. annularis* (2.4%), *Erythropodium* sp. (16.0%) and *Agaricia agaricites* (7.4%). The *Agaricia* Zone is restricted to the edge of the patch reef between 13 and 16 meters where the steepest slopes are present, but it also occupies regions as shallow as 10 meters.

Deeper Water Zones

The edge of the patch reef at depths below 16 and 28 meters is a gently inclined, mud-floored region characterized by mounds of burrowing organisms and coiled, whip-like antipatharians more than a meter high. Sponges, corals, and other reef organisms stop rather abruptly at the edge of the patch reef and visibility declines to less than 0.3 meter as the amount of suspended sediment increases markedly.

Distribution of Zones

The six biotic zones recognized at the Red Buoy Patch Reef generally appear to parallel depth contours (figure 1). However, the *Madracis* and Mixed Sponge Zones do not appear to be depth related and occur within a depth range from 7 to 18 meters. The distribution of these zones is patchy in comparison to the lateral continuity of the Massive Coral and *Agaricia* Zones. Although many of the zonal boundaries are distinct, overlap and transition between zones does occur, particularly in the southern part of the reef. Cross-sections across the patch reef are shown in figure 2.

The *Porites* Zone distribution appears to be controlled by depth. This zone is developed in shallow water, less than 7 meters, and is affected by currents and waves moving across the backreef area, producing a barren environment. Encrusting coralline algae are well-developed here. The coral *Porites* is adapted to the high energy, sunlit environment, and it is surprising that so few living corals of this genus are present. A large assemblage of *Diadema* feed on the algal encrusted rubble. Although this zone has excellent light penetration, the higher energy conditions appear to preclude much of the other biota. *Acropora palmata*, typically found in the shallow water Jamaican reef crest (1), is absent, but *Acropora cervicornis* is present in limited quantity.

The Mixed Sponge Zone covers a large area of the northwestern portion of the patch reef. The map (figure 1) illustrates that this zone is not found as a parallel band, but occurs only between the *Porites* Zone to the east and the *Madracis* patches to the west. The Mixed Sponge Zone contains the finest-grained sediment and is dominated by a diverse assemblage of sponges with corals occupying a subordinate position of abundance. A large amount of mud with minor skeletal sand from higher areas of the reef accumulates in and around the sponges in low areas that are protected from any appreciable currents or wave action. The high percentage of mud in suspension and in the fine-grained substrate is clearly responsible for the dominance of the sponge fauna. Reiswig (5) states that the filter feeding of sponges is superior to that of corals in turbid environments.

The Massive Coral Zone, dominated by large scleractinian corals, forms a band that parallels the Red Buoy "bank," but the zone is poorly developed or absent in the southeast. The boundary between the Mixed Sponge and Massive Coral Zones is transitional and difficult to define over a distance of 7 to 8 meters. Fewer corals occur on the eastern side of the bank, which may be the result of restricted circulation in that area. Many corals show a wide range of ability to handle fine-grained sediments. Hubbard and Pocock (6) have ranked Caribbean corals by their sediment rejection ability. Many of the corals present at the Red Buoy appear to consist of excellent sediment rejectors: *Montastrea* , *Colpophyllia*, and *Manicina*. Other corals that are efficient at removing sediments, but which are absent at the Red Buoy Reef, are *Diploria* and *Meandrina*.

The *Madracis* Zone occurs in irregularly distributed patches dominated almost exclusively by *Madracis mirabilis*. The patches occur at progressively greater depths to the west and are associated with upwelling springs. We have not measured the salinity of these springs, but they are brackish or of low salinity, being fresh to the taste. The clustering of *Madracis* about these springs in almost total exclusion to other biota, suggests that this is a case of competitive exclusion because of the more euryhaline nature of this coral. We did not find springs associated with all of the *Madracis* , so this is not a limiting factor, but may help explain the complicated distribution of the zone. It seems possible in fact, that the *Madracis* patches may have been continuous prior to the placement of the buoy anchor. Certainly, the area where the cement base of the anchor now stands was formerly part of a *Madracis* patch, and it is possible that adjacent areas were affected during the placement of the buoy. The Mixed Sponge Zone, then, may be a younger zone in the area, which may explain the anomalous distribution pattern. The distribution of the *Madracis* Zone is remarkable when it is recognized that the coral is best developed at depths of 30 to 60 meters on the forereef slope of the fringing-barrier reef (2).

The *Agaricia* Zone is dominated by *Agaricia lamarcki*, a deep water scleractinian (1, 2), as well as *Montastrea cavernosa* and the bivalves *Spondylus* and *Isognommon*. The distribution of this zone appears to be closely related to depth and light intensity. It forms a band 2 to 7 meters wide that parallels the contour of the bank along the west and south, and is more patchy to the northwest at depths of 13 to 23 meters. This wide range of depths may be related to light conditions. The areas to the north are generally less turbid and thus, have greater light penetration. The *Agaricia* Zone also occurs within the Massive Coral Zone, but only in areas where the slope of the substrate prevented mud accumulation.

Conclusions and Implications for the Fossil Record

Species	Zone				
	Porites	*Madracis*	Sponge	Coral	*Agaricia*
ALGAE					
Ceramium nitens	---	---	28.0(37.0/19.0)	8.2(-/16.4)	9.8(18.0/1.6)
Peyssoneillia? sp.	---	---	0.9(-/1.8)	---	---
PORIFERA					
Agelas sp.	---	---	1.9(-/3.7)	7.5(4.1/10.8)	---
Callyspongia pallida	---	---	1.9 (3.7/-)	0.2(0.4/-)	---
Gelliodes areolata	5.9(-/11.7)	2.7(-/5.3)	2.7(4.6/0.8)	0.3(-/0.5)	---
Haliclona dora	---	---	8.8(16.7/0.8)	7.7(8.8/6.6)	1.0(2.0/-)
H. erina	1.7(-/3.4)	---	0.6(1.2/-)	---	---
H. rubens	21.3(32.2/ 10.3)	7.6(15.2/-)	3.9(4.3/3.4)	0.4(0.7/-)	---
Ianthella sp.	---	---	---	---	0.4(-/0.8)
Mycale laevis	---	---	---	---	0.2(-/0.3)
Mycale sp.	1.7(-/3.4)	---	0.6(1.2/-)	---	---
Neofibularia nolitangere	2.2(4.4/-)	---	0.7(-/1.3)	---	---
Sigmadocia sp.	---	---	---	---	1.4(-/2.7)
Speciospongia vesparia	---	---	1.6(3.1/-)	13.7(27.4/-)	4.0(8.0/-)
Verongia sp.	---	---	0.6(1.2/-)	---	---
red encrusting sponge	---	---	1.6(3.1/-)	---	---
COELENTERATA					
Agaricia agaricites	2.2(4.4/-)	---	7.1(10.5/3.7)	17.8(21.8/13.7)	7.4(10.0/4.1)
A. fragilis	---	---	---	---	1.2(-/2.4)
A. lamarcki	---	---	---	---	32.8(8.0/57.6
Colpophyllia natans	13.7(6.7/20.7)	---	---	---	---
Eusmilia fastigiata	---	---	0.4(-/0.8)	---	---
Madracis mirabilis	---	86.6(84.8/ 88.3)	---	0.8(-/1.6)	---
Montastrea annularis	---	---	0.9(-/1.8)	3.9(-/7.7)	2.4(-/4.8)
M. cavernosa	---	---	---	5.8(8.6/3.1)	16.3(23.0/ 9.5)
Mycetophyllia aliciea	---	---	---	0.7(-/1.4)	---
Porites astreoides	11.1(22.2/-)	---	4.2(-/8.4)	---	---
P. furcata	---	---	0.6(-/1.1)	---	---
P. porites	1.7(3.3/-)	---	3.6(-/7.1)	---	6.4(12.0/0.8)
Scolymia cubensis	---	---	---	0.4(0.7/-)	---
Siderastrea siderea	1.1(2.2/-)	---	3.4(1.2/5.5)	1.7(2.7/0.8)	1.0(2.0/-)
Millepora alcicornis	---	---	0.4(-/0.8)	---	---
Condylactis gigantea	---	---	2.8(-/5.5)	1.3(2.7/-)	---
Erythropodium sp.	---	---	4.8(-/9.5)	7.7(5.3/10.1)	16.0(27.0/4.9
Eunicea sp.	---	---	2.0(-/3.9)	---	1.4(-/2.7)
Heteractis sp.	---	---	1.8(0.6/2.9)	3.4(-/7.3)	---
Ricordia sp.	---	---	---	---	0.2(-/0.3)
MOLLUSCA					
Isognommon alatus	3.4(6.7/-)	---	7.6(11.1/4.0)	12.5(1.4/24.9)	1.1(-/2.2)
Pinna sp.	---	---	---	2.0(4.1/-)	---
Spondylus americanus	---	---	---	3.4(6.8/-)	1.5(-/3.9)
ARTHROPODA					
Periclinenes sp.	---	---	---	0.2(0.4/-)	---
ECHINODERMATA					
Diadema antillarium	38.9(15.6/62.1)	---	5.4(4.9/5.8)	0.7(-/1.4)	1.0(-/1.9)
Eucidaris sp.	1.1(2.2/-)	---	---	---	---

Figure 3. Table of biota occurring within five biotic zones at the Red Buoy Patch Reef. Numbers are given as average zone percentage(transect 1 percentage/ transect 2 percentage).

The fauna of the Red Buoy Patch Reef forms a striking contrast to that of the Jamaican fringing-barrier reef. Low light intensities result from the great amount of suspended carbonate mud and particulate organic matter. There is a sparsity of shallow water corals that cannot tolerate fine sediments. The faunal association is one that normally occurs on the forereef slope of the fringing-barrier reef (2) at depths of greater than 35 meters, instead of the assemblage expected in a 6 to 25 meter lagoonal area. The results of this study should be considered when comparing ancient corals and coral zones with modern depth-related reef zones as has been attempted by some modern workers (7). This study emphasizes that caution must be applied before assigning absolute depth limits. We have demonstrated that coral growth forms and reef zonations typical of deep water can occur at considerably shallower depths given special conditions of turbidity, light intensity, salinity, and water circulation.

Many ancient patch reefs and organic buildups dominated by zoned sponge-coral associations have been reported from the rock record. Several of these are considered to be anomalous because they occur within rocks whose original textural features indicate fine-grained muddy substrates. Examples can be cited from the Ordovician (8, 9), the Devonian (10), the Carboniferous (11), the Permian (12, 13), the Triassic (14, 15), and the Jurassic (16). We feel that living reefs, such as the one we describe from Jamaica, are comparable to many of those in the rock record, and that they may provide insight into the biotic relationships of their ancient counterparts.

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