Hard Substrata Community Patterns, 1-120m, North Jamaica

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Tropical marine communities from shallow-water (<30 m) carbonate environments are often dominated by hermatypic scleractinian corals with lesser amounts of crustose coralline algae and endolithic demosponges. Living cover is typically high (80–100%). Along the north-central coast of Jamaica and at many western Atlantic sites, communities existing below 55 m inhabit a vertical to overhanging wall of reef limestone, the deep fore reef, which extends to approximately 130 m. At 60 m the community resembles that of shallower water, although scleractinians are less abundant and encrusting and erect demosponges are much more abundant. Coralline algae and macroalgae are also important space occupants at 60 m and living cover approaches 65%. Encrusting sponges and coralline, filamentous, and macroalgae predominate in the middle region of the deep fore reef. A low-diversity assemblage occupying 40% of the substratum and dominated by diminutive encrusting and endolithic demosponges and largely endolithic filamentous algae occurs from 100–130 m, the lower limit of the deep fore reef. Community structure and zonation on the shallower reefs is controlled by a number of biotic and abiotic factors, most notably predation/graazing, light intensity, and turbulence. On the deep fore reef, grazing and turbulence are greatly reduced. While reduced in intensity, light continues to exert a strong influence on community bathymetric zonation. Sedimentation also exerts an important control on the spatial distribution of the deep fore-reef biota with the most diverse assemblages flourishing in areas protected from sediment. Despite a regime of reduced disturbance in deep water, community diversity remains relatively constant to a depth of 90–100 m.

INTRODUCTION

Although hundreds of studies of tropical shallow-water (<30 m) marine communities from the Western Atlantic exist (see Milliman, 1973; Collin, 1978), studies of deeper environments, particularly those below 60 m, are much rarer (Ginsburg and James, 1973; Hartman, 1973; Lang, 1974; Lang et al., 1975; James and Ginsburg, 1979; Fricke and Meischner, 1985; and Littler et al., 1985) because of physiologic constraints on SCUBA diving and the expense of submersible time. This is unfortunate, as many of the marine sediments and biota preserved in the rock record are likely to represent depths in excess of 30–60 m. Further, the comparison of communities existing under greatly differing ambient environments (shallow and deep) will help elucidate the important controls on community structure.

Deeper sites differ from shallower reef sites in a number of important parameters, most notably, light and disturbance intensities, sedimentation rates, and abundance of low-angle substrata. These parameters may influence the structure of deep communities in a variety of ways: 1) Changes in both the intensity and spectral characteristics of light occur with increasing depth. Inasmuch as light may be considered as a resource for reef organisms such as algae, most corals, and many sponges (Huston, 1985), depth-related changes might be expected to influence the composition and diversity of benthic assemblages. 2) Many types of physical (e.g., daily wind-generated waves and, rarer, storm events, fluctuations in temperature, etc.) and biotic (predation/graazing) disturbance are reduced in intensity with increasing depth. Considering the important role assigned to disturbance in the regulation of diversity (Connell, 1978 and many others), the diversity of deeper settings might be expected to differ considerably from shallower sites. 3) Throughout the Caribbean, most sites in excess of approximately 50-60 m exhibit a vertical to nearly vertical submarine profile due to the cutting of seaciffs during the Wisconsin low stillstand at 100 m below present mean sea level (Goreau and Land, 1974; Liddell and Ohlhorst, 1981). The lack of extensive areas of low-angle hard substrata in deeper water influences the types of organisms capable of attaching to and growing on the deep reef. 4) Finally, when low-angle surfaces do occur on the deep reef, burial by sediment is a great problem for the epibenthos.

This study extends the knowledge of the shallow Jamaican
reefs, arguably among the most studied reefs in the world, to considerably greater depths (up to 120 m, which represents the lower limit of widespread suitable hard substrata for colonization by encrusting and endolithic benthos). Specific goals are to document hard substrata community zonation over the range of 1–120 m, examine depth-related trends in diversity over this range, and determine the effects of factors such as disturbance, light intensity, site microtopography, and sediment accumulation on community structure and diversity. These will enable the development of models for deeper-water carbonate-producing communities and the testing of hypotheses relating community diversity to disturbance intensity.

STUDY LOCALITY

Discovery Bay lies on the north-central coast of Jamaica at Lat. 18°30’N and Long. 77°20’W. The well-developed fringing reefs occurring along this coast display a striking, depth-related macrobionic zonation which has been described in several papers (Goreau, 1959; Goreau and Goreau, 1973; Kinzie, 1973; Lang, 1974; Bonem and Stanley, 1977; Liddell et al., 1984a,b; Huston, 1985; and Liddell and Ohlhorst, 1987). The fringing reefs studied occur on the West Fore Reef and are known as Watertower and Zingorro (A-A’) and Mooring One (B-B’, Figs. 1–2). Huston’s (1985 and unpublished) 0.5 and 5 m data and Liddell and Ohlhorst’s (1987) 15 m data were collected on Watertower Reef, which is located immediately east of and merges with Zingorro near the reef crest. The following succession of structural/geomorphic zones would be encountered along an onshore to offshore traverse across the West Fore Reef: back reef, reef crest, fore-reef terrace, fore-reef escarpment, fore-reef slope, deep fore reef, and island slope. Abrupt breaks in slope occurring along this profile (e.g. the fore-reef escarpment and deep fore reef) are interpreted as wave-cut seacliffs formed during Pleistocene low stillstands (Goreau and Land, 1974; Liddell and Ohlhorst, 1981).

METHODS

Field

Shallow-water census data were collected over the range of 1–30 m by divers using SCUBA. A chain method (Porter, 1972) in which a chain was draped over the reef and oriented perpendicular to the depth gradient and the number of chain links occurring over each substratum category recorded was used between 0.5 and 5 m (Huston, 1985). A linear point intercept method (Lucas and Seber, 1977; Eberhardt, 1978), in which a 10 m line with points located every 20 cm was draped over the reef and the identity of the organisms or substratum type occurring beneath each point recorded, was used between 15 and 30 m (Liddell and Ohlhorst, 1987). Up to 10 parallel lines, spaced at 1 m intervals and oriented perpendicular to the depth gradient, were observed at each site (Fig. 2). At 45 m divers using SCUBA conducted photo transects which were oriented perpendicular to the depth gradient. Color transparencies, illuminated by strobelight, of 0.14 m² areas were taken at 1 m intervals.

A Perry submersible (PC-8), owned and operated by Research Submersibles Ltd., Grand Cayman, was utilized in data collection over the range of 53–120 m on the vertical to overhanging escarpment of the deep fore reef. The submersible’s external camera and strobelight were used to conduct photo transects in which color transparencies of 0.14 m² areas were taken at 1 m spacings at each depth.

Laboratory

Photo census data were processed by projecting transparencies at natural size onto a screen with a fixed array of points
### Table 1—Bathymetric distribution of major taxonomic groups and site diversity*

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<th>Site†</th>
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<th>W³</th>
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<th>Z⁴</th>
<th>M⁴</th>
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<td>16.7</td>
<td>1.9</td>
<td>5.2</td>
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</table>

*95% confidence intervals in parentheses.
†W = Watertower, Z = Zingorro (deep fore reef begins at approx. 60 m), M = Mooring One (deep fore reef begins at approx. 50 m).
‡Data from Huston (1985 and unpublished), chain method.
§Data from Liddell and Olhore (1987), LPI method.
¶Diver transect reassessment.
©Submersible phototranssects.

(27 points, each with a 10 cm spacing) and the identity of the organism or substratum category occurring at each point recorded (planar point intercept method; Kinzie and Snider, 1978). Census data were used to determine community composition (larger taxa) and diversity at each depth (Table 1). Species number (S), dominance diversity (H’, nat. log; Shannon and Weaver, 1948), and evenness (J’, nat. log; Pielou, 1966), were employed as diversity indices. Diversity values so obtained must be viewed as approximations. The filamentous algal category represents multispecies aggregations that could not be identified from the slides. Also, sponge species separations are tentative, as spicule preparations have not yet been made; thus, some species may have been incorrectly "split" while others were incorrectly combined. Bathymetric trends in diversity, living cover, and distribution of particular taxa were tested with the Spearman Rank Correlation Coefficient (SRC). Cluster analysis (normalized Euclidean distance coefficient, unweighted centroid algorithm, Systat version 3.0) was used to discern zonation patterns.

Fore-reef sites are characterized by low water turbidity (light attenuation coefficient 0.06/m for the upper 30 m of the water column, Brakel, 1979). Although the attenuation (a combination of absorption and scattering) of sunlight by sea water is nonlinear in the upper 5 m of the water column, the
attenuation coefficient approaches a constant at greater depths (Jerlov, 1977). Therefore, Brakel’s (1979) attenuation coefficient was used to extrapolate irradiance values to a depth of 120 m in the water column. This exercise yielded a 1.0% of surface illumination value at approximately 65 m and a 0.05% value at 110 m. Irradiance values generated by this procedure are, of course, no substitute for in situ quantum irradiance measurements and must be regarded with caution.

RESULTS

It is appropriate to begin by pointing out that shallow reefs are far from the highly stable environments they were once considered. The reefs of the north-central coast of Jamaica, for example, have suffered two severe disturbance events this decade. The first was Hurricane Allen, which struck the north coast in August, 1980, and caused extensive damage to the shallow reefs (see Woodley et al., 1981; Ohlhorst and Liddell, 1981; and Liddell et al., 1984b for descriptions). The second event, the mass mortality of the urchin grazer, Diadema antillarum, occurred in August, 1983 while the reefs were undergoing a succession following the hurricane. The reduction in urchin densities from 14/m² at some sites to nearly 0.0/m² resulted in a rapid and dramatic increase in filamentous and erect macroalgal biomass which occurred at the expense of other benthos, such as corals, boring sponges, and crustose coralline algae (Hughes et al., 1985; Liddell and Ohlhorst, 1986). Inasmuch as the urchin did not occur in great numbers at depths in excess of 20 m, the effects of the urchin mass mortality were restricted to the shallower reefs. As of July, 1987, the shallow reefs have still not recovered from this perturbation (personal observation). The data we are presenting herein for shallow reef sites were collected prior to these disturbance events. For consistency, the present tense will be used in describing both shallow, now disturbed, and deeper reef sites.

Back Reef to Island Slope Traverse

The back reef or lagoon is an area of reduced coral growth due to high sediment production by macroalgae and high sediment resuspension caused by the burrowing activity of the ghost shrimp Callianassa (Aller and Dodge, 1974). The reef crest extends from the surface seaward to a depth of approximately 7 m and consists of large palmate colonies of the coral Acropora palmata, with branches oriented perpendicular to the incoming waves. The shallowest fore-reef sites (1–5 m) exhibit high rates of physical (turbulence) and biotic (largely grazing by urchins and, to a much lesser degree at Jamaica, fish) disturbance. Few corals possess the biomechanical adaptations (Shinn, 1963; Graus et al., 1977) necessary to survive in this environment and coral species diversity is, accordingly, low. The fauna is dominated by the coral A. palmata, crustose coralline algae, and boring clionid sponges; total faunal diversity is also low (Table 1).

The fore-reef terrace extends from 7 to 15 m and consists of large parallel lobes of coral oriented perpendicular to the reef crest and extending seaward at a moderate (15–20°) slope for approximately 200 m. These lobes are interrupted by sand channels, resulting in a spur-and-groove topography. These lobes or spurs of coral often rise up to 5 m above the surrounding sand and terminate in a steep (45°+) escarpment extending from 15 to 25 m. Fifteen-meter sites on the outer portion of the fore-reef terrace are dominated by corals exhibiting diverse morphologies, including mounds (Montastrea annularis), encrusting sheets (Porites astreoides), fingers (Porites porites), and branches (Acropora cervicornis). In addition to corals, boring sponges (largely clionids) and crustose coralline algae are important community components. Noncrustose algal biomass is very low. Turbulence and grazing by urchins still exert significant effects on the reef community at this depth. Coral species and total macrocommunity diversities are greatly increased over 5 m sites.

The landward portion of the fore-reef slope, which begins at 25–30 m depth, usually consists of a low-angle (5–20°) sand “moat” containing scattered coral heads. Coral cover increases by 30–35 m, often forming parallel lobes and occasional pinacles which may rise up to 10 m above the sand. At approximately 35 m the slope increases to between 45–60°. The fore-reef slope at 30–45 m is dominated by plate corals, largely Montastrea annularis, and various Agaricia species (Fig. 3). Demosponges and macroalgae, such as Lobofora and Halimeda, are important members of the benthos, while crustose coralline algae and boring clionid sponges are less abundant than at shallower depths. The decline in abundance of these groups on the fore-reef slope is attributed to a lack of suitable substrata, due to the absence of turbulence generated debris and the prevalence of plate-like coral growth forms with little exposed, bare skeleton (Liddell and Ohlhorst, 1987). In addition, the predominance of macroalgae over this range may negatively influence the abundance of crustose corallines. It should be noted that boring sponges attacking corals from the undersurface of plates would not be recorded using the above methods. Turbulence and grazing by urchins is much reduced.
relative to shallower reef sites. Although coral diversity is decreased somewhat relative to shallower sites, overall macrocommunity diversity is equivalent to that of 15 m sites.

A slope break occurring between 45 and 65 m, typically at 55 m, marks the beginning of the deep fore-reef “wall.” Although the faunal composition of the upper part of the deep fore-reef wall (55–60 m) is similar to that of the lower fore-reef slope, corals are less abundant while demosponges increase dramatically in abundance and macroalgae remain important community components (Fig. 4). By 70–75 m corals become extremely rare (observed by researchers, but not detected by photocensuses). Crustose coralline algae are abundant and macroalgae (largely various *Halimeda* species) are also common. Sclerosponges are common in more sheltered areas (Fig. 5). Community diversity is similar to that of shallower sites.

The slope of the wall decreases at a depth of 105 m and sediment accumulation on exposed surfaces becomes a major problem for the epibenthos. Endolithic algae and encrusting demosponges are the most important community components, while macroalgae and sclerosponges decrease greatly in abundance (Fig. 6).

The steep (60–90°) escarpment ends at approximately 120–130 m where the more gentle (20–45°) and sediment-covered island slope begins. Encrusting organisms are restricted to isolated blocks of talus derived from above.

**Bathymetric Trends in Community Composition**

Living cover is highest (82–100%) on the crest, fore-reef terrace, and upper (30 m) fore-reef slope (Table 1). On the mid- to lower fore-reef slope (45 m) and the upper- to mid-deep fore-reef wall (53–70 m), values for living cover range between 60–70%, while on the lower deep fore reef (105–120 m), living cover declines to 38–43%. There is a general decline over the range of 0.5–120 m (Fig. 7; SRC, p<0.01).

Coral abundance (Fig. 7) fluctuates between 28–62% over the range of 0.5–30 m, declines to 9–16% by 60 m on the upper deep fore-reef wall, and finally drops to near 0.0% by 75 m, although rare hermatypic and ahermatypic colonies occasionally occur below this depth. The decline in abundance with increasing depth is significant (SRC, p<0.01).

Crustose coralline algae exhibit a somewhat bimodal distribution (Fig. 7) reaching highest abundances at 0.5–5 m (33–36%) on the fore-reef terrace and at 75–90 m (18–19%) on the deep fore reef. At 30–53 m on the fore-reef slope coralline algae occupy only 3–15% of the substratum. Overall, coralline algae are negatively correlated with depth (SRC, p<0.05).

Noncrustose algae, including both filamentous-endolithic
FIGURE 7—Bathymetric distribution of biotic cover (percent of available substratum).
algae (greens and blue-greens and, in shallow-water, reds) and macroalgae (greens and browns) reach their peak abundance (30–47%) at 45 m (Fig. 7), although they are still significant community components (16%) at 120 m. The increase in non-crustose algal abundance to 45 m is significant (SRC, p<0.05) while the decrease from 45 to 120 m is slightly less so (SRC, p<0.10). Shifts in the relative abundances of the two groups do occur, with macroalgae predominating over the range of 30–75 m and filamentous-endolithic algae from 75–120 m. Macroalgae increase significantly in abundance to 45 m (SRC, p<0.05) and then decline to 90 m (SRC, p<0.01). Filamentous-endolithic algae are positively correlated with increasing depth over the range of 0.5–120 m (SRC, p<0.01).

Scleropsonges (Fig. 7) exhibit the most restricted range of the major community components, occurring in relatively exposed (noncryptic) locations only from 60–90 m. A peak abundance of 7% occurs at 90 m. Scleropsonges are known from shallower cryptic settings such as caves and the undersurfaces of foliaceous corals (Hartman and Goreau, 1970; Jackson et al., 1971).

Demopsonges exhibit a somewhat bimodal distribution with an overall slight trend of increasing abundance with depth (SRC, p<0.10, Fig. 7). If, however, endolithic cianthids are considered separately from erect or encrusting demopsonges, the former decrease significantly with increasing depth (from 20.0% to 0.0%; SRC p<0.01) while the latter increase significantly (from 0.0 to 20.0%; SRC, p<0.01) and remain important community components to 120 m (Table 1).

Cluster analysis reveals a well-defined bathymetric zonation (Fig. 8). Two major groupings were delineated with their boundary occurring between 30 and 45 m. Within the deeper cluster the 45 m fore-reef slope sites were most distinct while deep fore reef sites were subdivided into fore-reef slope—deep fore-reef break (53–60 m), upper deep fore reef (68–75 m), and lower deep fore reef (90–120 m). From onshore to offshore the following groups dominate each zone (listed in order of declining importance): corals, coralline algae, boring sponges (0.5–22 m); macroalgae, corals, coralline algae (45 m); sponges, corals, macroalgae, coralline algae (53–60 m); sponges, macroalgae, coralline algae, filamentous algae (68–75 m); and sponge, filamentous algae (90–120 m). In the three deepest zones the dominant groups are approximately coequal.

Bathymetric Trends in Diversity

At the macrobiota level (corals, noncoral cnidarians, demosponges, scleropsonges, macroalgae, etc.), species diversity and evenness (S, H', J'; Table 1, Fig. 9) is low at 0.5–5 m, increases by 15 m, and continues to increase to 53 m (SRC, p<0.05), finally declining to 120 m (SRC, p<0.05 for H' and J' only). Community diversity is not correlated with percentage of living cover. Although total community diversity is relatively constant over a broad bathymetric range (15–106 m), major shifts in species diversity of the larger taxonomic categories occur. For example, coral species diversity declines rapidly below 50 m but is offset by an increase in sponge diversity on the deep fore reef.

Effect of Microtopography

Microtopographies are inequally distributed over the bathymetric range of our study. Exposed low-angle surfaces preclude above 60 m, while vertical exposed or sheltered (beneath overhangs) surfaces predominate on the upper portions of the deep fore reef. On the lower portions of the deep fore reef, vertical to moderately inclined exposed surfaces predominate.

On the deep fore reef, vertical sites consistently exhibit the highest percentage of living cover, while low-angle sites consistently exhibit the lowest percentage of living cover. This effect is largely caused by the accumulation of sediment on low-angle surfaces. While vertical sheltered sites typically have higher percentages of living cover than vertical exposed sites, no consistent differences exist between low-angle sheltered and exposed sites.

Microtopography also influences the irradiance available to the benthos. Brakel (1979) demonstrated that a north-facing vertical surface would receive only 25% and a 60° slope only 50% of the illumination received by a horizontal surface. Thus, the estimated depth of the 1.0% of surface illumination value for the water column (65 m) must be shifted upward to approximately 55 m for a 60° surface on the upper deep fore reef or lower fore-reef slope and to 45 m for a vertical surface. Similarly, the depth of the 0.05% value must be shifted upward from 110 m in the water column to approximately 90 m for a vertical surface and to 100 m for a 60° surface.
DISCUSSION

Controls on Community Composition and Diversity

The depth-related biotic zonation shown by these reefs is the result of the complex interplay between a variety of physical/chemical parameters and biotic interactions. In areas located above wave-base (approximately 20–30 m), depth-related shifts in reef community composition are most likely influenced by environmental turbulence (Geister, 1977). Light levels will probably not limit coral species diversity on the shallower (<30 m) reefs (Loya, 1976). Turbulence will interact with the biomechanical characteristics of various coral species (e.g., excluding all but Acropora palmata from the very shallow—1–5 m—fore reef). Another, more subtle, effect of turbulence on reef community composition may be the generation of hard substrata by the toppling and fragmentation of coral colonies in shallow water. Such hard substrata are rapidly colonized by coralline algae and boring sponges (Ohlhorst and Liddell, 1981; Liddell et al., 1984b), which are important components of shallow reef communities. The inverse correlations of these groups with depth suggest that the lack of turbulence-generated hard substrata may account for their much reduced abundance on the fore-reef slope (30–55 m).

Diadema grazing has been shown to influence the macroalgal community structure of coral reefs markedly and also to affect sessile epibenthic invertebrates (Sammarco et al., 1974; Carpenter, 1981). The increase in macroalgal abundance on the fore-reef slope is most likely an effect of the decrease in Diadema abundance below 20–30 m (Liddell and Ohlhorst, 1987). The causal factors behind Diadema’s depth limitation are unknown. The bathymetric distribution of the intensity of predation or grazing by other groups is not well known, although there is some evidence that the effects of fish (Bakus, 1969, 1972) and other invertebrates, such as the polychaete Hermophis and the gastropod Coralliophila (Ott and Lewis, 1972), are most important in shallow water. Personal observations at Jamaica support these findings.

On the wall of the deep fore reef, turbulence and grazing are likely to generate relatively little effect on the biota; instead, light intensities and sedimentation are likely to be important controllers of community composition. Light intensities decline with increasing depth and are also influenced by site microtopography (degree of inclination and sheltered or exposed) and orientation. Sedimentation is also influenced by site microtopography, with highest accumulations occurring on exposed, low-angle surfaces.

The community composition of the deep fore reef differs greatly from that of shallower reef sites. Whereas the shallow reef (5–30 m) is dominated by scleractinians, crustose coralline algae, and endolithic demosponges, the deep fore reef (60–120 m) is dominated by erect or encrusting demosponges, crustose coralline algae, and noncrustose (macro- and filamentous) algae. In terms of macrocommunity diversity, the deep fore reef is very similar to shallower sites. As such, the deep fore-reef diversity data do not appear to follow the predicted trends of the intermediate disturbance hypothesis as applied to coral reefs. Sites with intermediate levels of disturbance should exhibit the highest diversities as disturbance prevents

exclusion by competitively superior species. The deep fore reef appears to be an environment of reduced disturbance as turbulence and grazing, among the major sources of disturbance on the shallow reefs, are absent or reduced. Deep fore reef community diversity, however, is as high as or higher than that of much shallower sites (e.g., 0.5–30 m). Perhaps other factors, such as sedimentation or detachment from the steep escarpment of the deep fore reef are serving to reduce competitive exclusion and, thus, promote diversity. The former, however, is unlikely to do so as diversity is highest in areas little affected by sedimentation (e.g., vertical sheltered sites). Furthermore, while the latter may affect corals and erect demosponges on the upper part of the deep fore reef, it is unlikely to influence the tightly encrusting demosponges on the middle and lower portions of the deep fore reef.

The deep fore reef is not a uniform environment, however, as light intensity does decrease with increasing depth. If light is viewed as a nutritive resource for photosynthetic organisms (cf., Huston, 1979, 1980, 1985; Tilman, 1982), perhaps the diversities of the deep fore-reef communities reflect the mediating effects of intermediate resource levels on competition by the benthos despite very low levels of disturbance.

Other Studies of Deep-Water Communities

Studies of deep-water (>60 m) tropical marine communities are rare. Even more so are quantitative holistic studies of deep-water communities. The earliest attempts to utilize submersibles in the study of Caribbean deep-water communities were conducted at Belize (Ginsburg and James, 1973; James and Ginsburg, 1979) and Jamaica (Hartman, 1973; Lang, 1974; Lang et al., 1975). These studies were non-quantitative, yet provided important documentation on the lower depth limits of many taxa. In particular, various algae and hermatypic corals were found to extend to much greater depths than previously recognized. For example, the hermatypic coral Agaricia frigida was shown to extend to at least 97 m at Jamaica (Lang, 1974) and 103 m at Belize (James and Ginsburg, 1979). Furthermore, crustose coralline algae and filamentous algae were found to extend to 175 m at Jamaica (Lang, 1974) and crustose coralline algae to 250 m at Belize (James and Ginsburg, 1979). The importance of sclerosponges as primary deep-water framework constructors was documented by Lang et al. (1975).

Fricke and Meischner (1985) examined the bathymetric distribution of corals over the range of 0–79 m at Bermuda and found coral diversity (H') to be relatively constant (1.50–1.75) with only a slight increase over the range of 0–39 m. Diversity decreased rather sharply to 1.2 by 49 m and finally to 0.0 by 79 m due to a lack of suitable hard substrata. The deep-water (>60 m) hermatypic association consisted of Montastrea cavernosa, Agaricia frigida, and Scolymia cubensis, with M. cavernosa occupying the greatest amount of space and being the only coral to extend below 70 m (to 78 m). Although the photic zone limit (i.e., the compensation point where photosynthesis equals respiration, normally regarded as 1% of surface illumination; Ryther, 1956) did not occur until 100 m, corals were restricted to much shallower depths due to lack of suitable substrata and competition with macroalgae. At Jamaica, corals did not extend in abundance below 60 m even though suitable substrata were available considerably below this depth. This relatively shallow upper limit is consistent with the calculated quantum irradiance available on the very steep deep fore reef (1% level occurring at 55 m). M. cavernosa and Agaricia species were also the most abundant deep-water corals at Jamaica.

Littler et al. (1985) concentrated on the algae occurring on the steep face of a seamount off San Salvador Island, Bahamas. From 81 m (the top of the seamount) to 268 m, the algal community complexity and spatial heterogeneity decreased with increasing depth. The brown, erect macroalga Lobofora variegata predominated from 80–88 m, occupying a mean of 59.4% of the substratum. Halimeda copiosa dominated the algal community over the range of 117–130 m, accounting for up to approximately 20% coverage. Two green algae occurred abundantly from approximately 130–157 m and the green, rock-boring alga Ostreobium occurred as deep as 210 m. Coralline algae dominated between 210–268 m and occupied from 5% to over 20% of the substratum from 80–268 m. Encrusting sponges were found to be the predominant organisms from 268–520 m.

The deepest occurring coralline alga was at 268 m. Significantly, this alga occurred at a light intensity of 0.0005% of surface illumination, considerably below the generally accepted lower limit (1%) of the photic zone. In addition, fleshy macroalgae were found to extend to a 0.05% level. At Jamaica Lobofora and Halimeda are also important macrophytes, but predominate over a much shallower depth range. At Jamaica coralline algae were also found to extend to greater depths than macroalgae and sponges eventually replaced both of these groups as dominant, although the "zone" boundaries are shifted considerably upwards there.

Studies of deep-water communities from non-western Atlantic sites include Fricke and Schuhmacher (1983) and Hills-Colinvaux (1986). The former examined the distribution of corals over the range of 0–145 m along the Sinai coast of the Red Sea. One hundred thirty hermatypic coral species were found to occur over the range of 10–30 m while a total of only forty-seven species occurred below 50 m and nine species below 100 m. A single species occurred below 110 m. At this locality the 1% light level occurred at 100 m. The occurrence of such a high number of hermatypic species below 70 m contrasts sharply with the Western Atlantic settings (Jamaica and Bermuda). Also, no individual coral or small group (e.g., M. cavernosa and Agaricia species) dominated the deep Red Sea assemblage like in the Western Atlantic.

Hills-Colinvaux (1986) concentrated on the distribution of algae, chiefly Halimeda, over the range of 30–367 m on the steep fore reef at Eniwetok Atoll. From 30–65 m the biota was composed of hermatypic scleractinians, Halimeda, and crustose coralline algae. From 65–110 m Halimeda dominated the assemblage, although corals were also present. Few or no corals extended below 90 m while Halimeda reached 30% cover above 90 m and 10–25% cover between 90–110 m, finally decreasing to 0% below 140 m. Finally, Hills-Colinvaux noted that, while present, sclerosponges were not as abundant as at Jamaica. The deep-water zonation at this site is similar to that at Jamaica, although the transition to the coralline algal
dominated community occurred at a much shallower depth at Jamaica.

Implications for Studies of Ancient Hard Substra Communities

This study provides several implications for the paleoecological interpretation of ancient hard substrata communities. Most notable is the trend for skeletoned communities to dominate in shallow water and less skeletonized communities to dominate in deep water. The preserved assemblage would show an apparent decrease in diversity in deep water, accompanied by a decline in percentage of living cover. In reality, percentage of cover and diversity of the deeper communities may have been as high as or higher than shallower sites. Another important consideration is the high abundance of photoautotrophic organisms at much greater depths than normally predicted. This has implications for the reconstruction of trophic pathways in ancient deep-water communities. Also, as endolithic algae were found to be abundant at 120 m, this requires a downward shift in the generally accepted lower depth of prolific algal microboring, which has important paleobathymetric ramifications. Finally, the effect of microtopography has been demonstrated to exert an important control on the density (percent living cover) of hard substrata communities.

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REFERENCES

LIDDELL, W.D., and OHLHORST, S.L., 1986, Changes in benthic community composition following the mass mortality of Diadema at Jamaica:
What could be more comforting, what more convenient for human domination, than the traditional concept of a young earth, ruled by human will within days of its origin. How threatening, by contrast, the notion of an almost incomprehensible immensity, with human habitation restricted to a millimicrosecond at the very end!

—Stephen Jay Gould