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COMPARISON OF WESTERN ATLANTIC CORAL REEF COMMUNITIES

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ABSTRACT

The majority of Western Atlantic coral reefs are remarkably similar in terms of the coral species present at most sites (the exclusion of cold-intolerant taxa, such as Acropora and others, from Bermuda and the Flower Gardens is an exception). Localities differ greatly, however, in relative abundance of coral species and coral diversities (H'). The former cannot be readily related to geographic location, indicating the presence of a great degree of heterogeneity within the province which is due to differences in ambient environments and, perhaps, stochastic processes. Coral species diversity exhibits distinct geographic trends with the lowest values occurring at the southern (Colombian and Venezuelan coastal areas), northwestern (Campeche Bank, northern Gulf of Mexico) and northeastern (Bermuda) margins of the province. This pattern appears to be largely mediated by temperature, not restriction of larval dispersion. Finally, localities also differ in relative abundance of sessile benthic community components in addition to corals.

INTRODUCTION

The Western Atlantic Reef Province encompasses a geographically diverse area, including the Caribbean and Antilles, South Florida and the Bahamas, the Gulf of Mexico, Bermuda, and Brazil (Fig. 1). If the outliers of Brazil (23°S) and Bermuda (32°N) are omitted, the area spans some 17 degrees of latitude from the Caribbean coast of South America (11°N) to the northern Gulf of Mexico (28°N). Of the abundant studies dealing with Western Atlantic reefs only a relatively small number provide quantitative data on sessile benthic community composition. Of these, most are concerned only with corals, are restricted to narrow depth ranges, or do not present their data in such a way as to allow comparisons between sites.

The present paper incorporates the findings of other authors with our census data collected at five Western Atlantic reef sites in an attempt to determine geographic trends in coral species diversity and relative abundances as well as geographic trends in the relative abundances of various larger taxonomic groups of sessile benthos. Included are the Florida-Bahamian, Bermudan, Gulf of Mexico, and Caribbean-Antillean areas of the Western Atlantic Province. Sites vary from mainland localities (Colombia, Q. Roo, SE Florida, Venezuela) to large (Jamaica, Puerto Rico), relatively small (Barbados, Curacao) and tiny (Alacran, Triangulos Oeste) islands.

STUDY LOCALITIES

Census data were collected at Colombia, Curacao, and Barbados in 1977; at Alacran on the Campeche Bank in 1985; and at Jamaica at various intervals between 1980 and 1984 (Liddell et al. 1984, Liddell & Ohlhorst 1987; Fig. 1). With the exception of the Alacran data, our data were collected prior to several of the major disturbance events which have affected the Western Atlantic in recent years, Hurricane Allen in 1980 (Woodley et al. 1981), the mass mortality of the urchin Diadema antillarum in 1983 (Lessios et al. 1984), and the widespread bleaching of corals in 1987-1988 (Roberts 1987).

Localities were the following: at Jamaica, the West and East Fore Reefs in the vicinity of Discovery Bay (see Liddell & Ohlhorst 1987, their

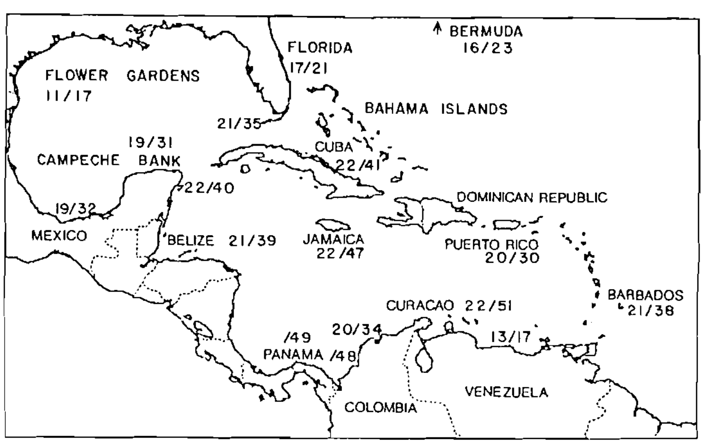

Figure 1. Western Atlantic Reef Province (modified from Atwood et al. 1988). Number of genera/species as determined from literature review plotted.

Fig. 1); at Curacao, the fringing reef just north of Piscaderabaai (see Bak 1977, his Figs. 1 and 2); at Alacran, the southeast corner, near the "boilers" and a site 4km north along the barrier near several shipwrecks and 2 km south of the prominent surge channel (see Kornicker & Boyd 1962, their Figs. 1 & 2); at Santa Marta, Colombia, Punta de Betin and the nearby island of Morrito (see Antonius 1972, his Fig. 1); at Barbados, the submerged barrier reef located immediately in front of the Bellair's Research Institute and Ott's (1975) Nurse's Jetty site (see Ott 1975, his Fig. 1). Jamaica and Alacran represent windward, the other sites leeward, settings. For general descriptions of these sites refer to Antonius (1972) for Colombia; Macintyre (1967) and Ott (1975) for Barbados; Bak (1977) for Curacao; Liddell et al. (1984) for Jamaica; and Logan (1969) and Chavez et al. (1985) for the Campeche Bank.

METHODS

Census data were collected via a linear point intercept method (Liddell & Ohlhorst 1987). Species number (S), dominance diversity (H', nat. log), evenness (J', nat. log), and the total number of coral species encountered during quantitative censusing over the range of approximately 0-30m at a locality were employed as diversity indices. The latter was felt to be a better indicator of locality diversity than species lists, which are strongly biased by the number of studies conducted at a locality. Correlations were tested with the Spearman Rank Correlation Coefficient (SRC). Q-mode cluster analyses (Normalized Euclidean Distance Coefficient, UPGMA algorithm) were used to construct groupings of localities. To allow comparisons between the widest number of sites within a limited number of pages and to eliminate the additional complexity of bathymetry, we will concentrate on 15m sites. Also, unfavorable sites with high sedimentation rates (e.g. Loya's 1976 West Reef site at Puerto Rico and Liddell et al.'s 1984 bay site at Jamaica) or lacking suitable hard substrata (e.g. Fricke and Meischner's 1985 $\geq$ 45m Bermudan sites) were excluded when data from more equitable sites were available.

RESULTS

Coral Species Distributions and Diversity

Coral species lists are quite similar for the Florida-Bahamian and Caribbean-Antillean regions when sufficient numbers of studies are conducted (based on review of the reef literature and personal observations from numerous localities). Forty to fifty 'hermatypic' scleractinian species (distributed among 22 genera) are known from most localities in the above regions. The Flower Gardens and Bermuda, however, differ from the above in lacking cold-intolerant corals, such as Acropora species, and possess depauperate scleractinian faunas of 17 and 23 species (11-12 genera), respectively (Bright et al. 1984). In addition, localities from the southern Gulf of Mexico (Veracruz and the Campeche Bank) appear somewhat impoverished, possessing 30 to 35 species (19 genera; Fig. 1).

Data on the relative abundance and diversity of coral species differ greatly between Western Atlantic localities (Table 1). Q-mode cluster analyses reveal no clear zoogeographic trends in relative abundances, however. For example, SE Florida was separated from other northern localities (Flower Gardens and Bahamas), the Greater Antillean localities (Jamaica and Puerto Rico) did not join together, and southern localities (Colombia and Venezuela) were also distinct from each other. Furthermore, two Q. Roo sites separated by 5 km (Puerto Morelos and Finduvet - Table 1 and Jordan et al. 1981) and two Jamaican sites separated by only 1km (Table 1) did not join. This indicates a great deal of heterogeneity in coral community compositions,

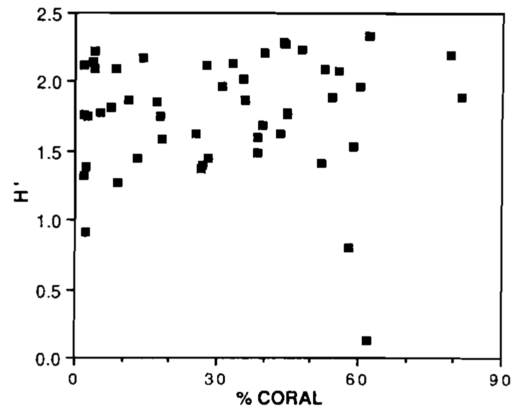

Figure 2. Plot of coral diversity (H') versus abundance (% of bottom). The two lowest H' values are from 0.5-5m sites at Jamaica. Includes additional sites from localities and studies cited in table 1.

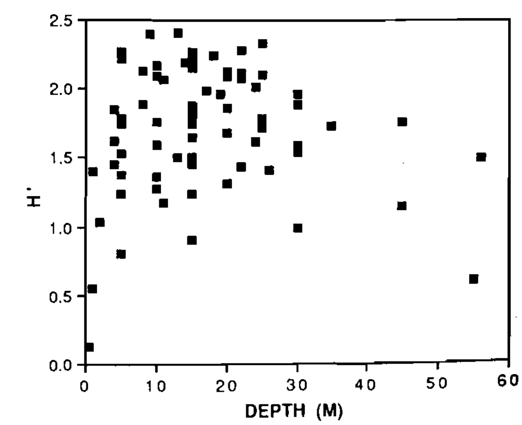

Figure 3. Plot of coral diversity (H') versus depth. Data from localities cited in table 1. Only sites possessing suitable hard substrata are included.

Table 1. Coral species diversity and relative abundance (% of corals) at approximately 15m.

Site:	BAR[1]	CUR[1]	COL[1]	ALA[2]	WJA[3]	EJA[4]	FLA[5]	FG[6]	PR[7]	VEN[8]	QR[9]	BAH[10]	BER[11]	SC[12]
N (points):	110	80	83	81	214	360	?	23*	14*	2179	?	46*	?	8
Acropora cervicornis	0.0	0.0	0.0	0.0	45.3	16.9	0.5	0.0	0.0	0.0	1.4	0.0	0.0	0.0
Agaricia agaricites	1.8	28.8	5.5	0.0	20.3	13.6	5.6	1.9	12.0	1.3	1.4	10.6	0.0	15.9
Agaricia lamarcki	0.0	0.0	3.4	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.3
Colpophyllia amaranthus	6.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Colpophyllia breviserialis	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Colpophyllia natans	4.5	8.8	5.5	4.9	1.1	1.9	1.3	14.0	5.7	3.8	1.4	0.0	0.0	3.1
Dendrogyra cylindrus	4.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dichocoenia stellaris	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dichocoenia stokesi	0.0	0.0	0.0	4.9	0.0	0.6	5.6	0.0	0.5	3.8	7.2	5.5	0.5	2.9
Diploria clivosa	0.0	0.0	0.0	0.0	0.0	0.0	20.0	0.0	0.9	5.1	0.0	0.0	0.0	0.0
Diploria labyrinthiformis	3.6	0.0	0.0	0.0	0.4	1.1	0.5	0.0	0.5	0.0	0.0	0.0	21.4	5.5
Diploria strigosa	7.3	1.3	2.8	8.6	0.0	3.1	0.0	18.3	1.8	10.1	7.2	0.0	42.9	2.6
Eusmilia fastigiata	0.0	8.8	0.7	0.0	0.4	0.0	1.3	8.8	2.9	0.0	1.4	0.0	0.0	0.0
Favia fragum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.5	0.0
Helioseris cucullata	0.0	0.0	0.0	1.2	1.0	1.9	0.0	0.0	4.8	0.0	1.4	0.0	0.0	0.7
Isophyllia sinuosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.5	0.0
Madracis decactis	0.0	18.8	3.4	1.2	1.5	1.7	0.5	1.9	0.0	0.0	0.0	0.0	0.5	13.4
Madracis mirabilis	0.0	3.8	0.0	0.0	7.6	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Manicina areolata	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.7	2.5	0.0	5.8	0.0	0.0
Meandrina meandrites	10.9	3.8	2.1	1.2	0.7	1.9	5.6	0.0	2.0	1.2	7.2	0.0	0.5	4.0
Montastrea annularis	11.8	7.5	2.1	13.6	6.1	30.6	20.0	48.5	15.2	0.0	34.0	44.7	10.7	12.0
Montastrea cavernosa	25.5	5.0	65.5	30.9	0.0	3.9	20.0	8.1	29.1	3.8	34.0	9.1	7.1	14.2
Mussa angulosa	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.9	1.3	0.0	0.0	0.0	0.2
Mycetophyllia ferox	0.0	1.3	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.2
Mycetophyllia lamarckiana	0.0	0.0	0.0	0.0	0.0	0.0	5.6	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Oculina diffusa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8	0.0	0.0	0.0	0.0
Phyllangia americana	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Porites astreoides	4.5	1.3	0.0	0.0	9.8	3.1	5.6	4.1	3.6	5.1	1.4	4.5	17.9	8.5
Porites furcata	1.8	5.0	0.0	0.0	2.6	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Porites porites	0.0	0.0	0.0	1.2	4.1	1.1	0.0	0.0	3.6	11.4	0.0	0.0	0.0	0.0
Siderastrea radians	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.2	1.3	0.0	0.0	0.0	0.0
Siderastrea siderea	15.5	5.0	1.4	28.4	1.3	9.4	1.3	2.7	7.1	34.2	7.2	20.0	0.0	6.3
Scolymia lacera	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.5	0.0
Solenastrea bournoni	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0
Solenastrea hyades	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	5.1	0.0	0.0	0.0	0.0
Stephanocoenia intercepta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0
Stephanocoenia michelinii	0.9	1.3	3.4	0.0	1.7	3.1	1.3	0.4	4.5	0.0	1.4	0.0	0.5	1.8
Species no.	14	14	13	12	15	17	19	11	20	--	13	--	13	17
H'[13]	2.27	2.21	1.45	1.86	1.87	2.23	2.25	1.69	2.20	--	1.81	--	1.65	2.47
J'	0.86	0.84	0.56	0.75	0.69	0.79	0.73	0.70	0.82	--	0.71	--	0.65	0.87
Total species no.[14]	21	21	14	17	22	22	21	11	21	18	21	28	17	25

[1] Each was a 15m site.
[2] A 20m site.
[3] A 15m site on the West Fore Reef at Discovery Bay, Jamaica (Liddell & Ohlhorst 1987).
[4] A 15m site on the East Fore Reef at Discovery Bay (Liddell et al. 1984).
[5] A 16-20m site, SE Florida, N of Miami (Goldberg 1973).
[6] A 20m site, East Flower Garden Reef, N. Gulf of Mexico, *N = no. of 8m transects (Bright et al. 1984). Data modified by removal of Millepora. Agaricia and Colpophyllia species not separated in their table.
[7] A 11-17m site, East Reef, Puerto Rico, *N = no. of 10m transects (Loya 1976).
[8] Average of many 0-15m sites in the Gulf of Cariaco, Caribbean Venezuela (Antonius 1980). Data modified by removal of Millepora. Due to the depth range encompassed and the combination of many sites, the diversity of this locality is probably inflated.
[9] A 15m site at Puerto Morelos, Q. Roo, Caribbean coast of Yucatan Peninsula, Mexico, (Jordan et al. 1981). Data modified by removal of Millepora.
[10] Average of many localities in the Bahamian region over the range of 14-38m, typically 15m, *N = no. of 10m transects (Bunt et al. 1981). The diversity is probably inflated.
[11] A 10-19m site at Bermuda (Fricke & Meischner 1985). Data modified by removal of Millepora.
[12] A 18m E wall site at St. Croix, *N = no. 10m transects (Rogers et al. 1984).
[13] Additional diversity data available for Caribbean Panama (H'= 1.24-1.51 at 15m, modified to nat. log, from Porter 1972).
[14] Coral species encountered in transects over the range of approximately 0-30m (BAR, 15-30m; COL, 10-15m; CUR 10-30m; ALA, 10-30m; WJA, 0-30m; EJA, 5-24m; FLA, 9-30m; FG, 20-26m; PR, 8-20m; VEN, 0-15m; QR, 5-20m; BAH 13-38m, average of many sites; SC 9-37m). Additional data,available from Dry Tortugas, Florida Keys (25 species from 0-17m, Porter et al. 1976), Enmedio Reef, Veracruz, Mexico (15 species from 11-17m, Rannefeld 1972), and Triangulos Oeste, Campeche Bank (10 species from approximately 0-25m, Chavez et al. 1985).

Table 2. Relative abundance of larger taxonomic categories at approximately 15m. Unless noted otherwise, localities are the same as in Table 1.

Site:	BAR	CUR	COL	ALA	WJA	EJA	FC[1]	VEN[2]	PR[3]	VER[4]	BAH[5]	BER[6]	QR[7]	SC[8]
N (points):	246	200	518	728	606	748	23*	5200	14*	?	46*	?	560*	8*
Corals	44.7	40.0	28.0	11.1	35.9	48.1	39.7	23.1	79.6	20.0	11.5	18.0	7.6	24.0
Noncoral cnidarians	0.8	3.0	0.4	5.4	3.8	2.7	--	11.6						
Fleshy sponges	3.3	5.0	1.7	3.4	1.7	4.3	--	2.2						
Boring sponges	1.6	6.5	1.0	1.8	20.0	7.8	--	*						
Coralline algae	6.5	8.0	7.3	5.2	13.3	9.2	14.9	**						
Macroalgae	0.0	0.0	0.0	45.6	2.8	0.7	--	18.2						
Filamentous algae	0.0	1.5	1.0	1.9	5.2	3.5	--	**						
Misc. living	0.0	1.5	0.6	1.2	1.1	3.3	--	--						
Bare hard substrata	9.3	12.0	44.2	7.0	12.4	9.4	--	45.0						
Sand/mud	33.7	22.5	15.8	17.3	3.8	11.0	15.0	--						
Total living	57.0	65.5	40.0	75.7	83.8	79.6	--	55.0						

[1] Data of Bright et al. (1984) modified by conversion from percent of hard substrata to percent of total bottom and removal of Millepora from corals. *N = no. 8m transects.
[2] Data of Antonius (1980) modified by conversion from percent of living to percent of total bottom and removal of Millepora from corals. *His sponge category consists of all sponges, including boring taxa? **His algae category consists of all algae, including crustose corallines.
[3] *N = no. of 10m transects.
[4] An 11-17m site, Enmedio Reef, off Veracruz, Mexico, Gulf of Mexico (Rannefeld 1972).
[5] *N = no. of 10m transects.
[6] A 3-5m site at Bermuda (Dodge et al. 1982).
[7] Percent of living not total bottom, *N = no. of 2.7cm links.
[8] *N = no. 10m transects.

occurring at various geographic scales. The two sites which were most distinct from all others, Colombia and West Jamaica, are characterized by, respectively, high dominance by Montastrea cavernosa and Acropora cervicornis.

For localities near the center of the province, at 15m coral H'values are typically near 2.0 and the total number of species encountered during censusing at a locality is 21-22 (Table 1). Sites on the Campeche Bank, the Flower Gardens, Bermuda, Colombia, and Venezuela (the latter two localities are represented by coastal settings) exhibit reduced diversity relative to the other Western Atlantic sites studied. Coral diversity is not significantly correlated with coral abundance (% cover: Fig. 2). Although coral diversity is low in very shallow ($\leq$ 5m) water, it is quite constant over the range of 10-30m (and deeper if suitable substrata are available) (Fig. 3).

Abundances of Larger Taxonomic Categories

Cluster analyses of the relative abundances of larger taxa were restricted to five sites (Barbados, Colombia, Curacao, and West and East Jamaica, Table 2) due to the paucity of such data in the reef literature. Alacran was omitted due to the exhibition of high algal/coral ratios, presumably, following the mass mortality of Diadema. Colombia is the most distinct locality, its separation from the other localities resulted from relatively high amounts of nonliving bottom. The two Jamaican sites differ from Curacao and Barbados in possessing relatively high living covers.

Sites from the Greater and Lesser Antilles and Curacao exhibit the highest amounts of coral cover (36-79%), the South American coastal settings have somewhat lower coral cover (23-28%), and the more northern (Bahamas and Bermuda) and more western (Q. Roo, Campeche Bank, Veracruz) localities possess the lowest coral covers (7-22%, Table 2). The Flower Gardens are an exception in that they show a high coral cover (40%), despite their northern location (28°N).

DISCUSSION

Numerous papers have described Western Atlantic reef communities (see Glynn 1973, Milliman 1973, and Colin 1978 for summaries). These studies tend to document depth-related coral zonations which are similar to Goreau's (1959) zonation model for Jamaica. Additionally, species lists appear to be roughly comparable for most localities in the Florida-Bahamian and Caribbean-Antillean regions. The depauperate appearances of many localities are often an artifact of insufficient study. This uniformity of coral species distributions is in contrast to that of fish and various other invertebrate groups which exhibit pronounced endemism, enabling the delineation of Antillean/West Indian and Caribbean (Central and S. American) faunal provinces (Briggs 1974). Such widespread homogeneity of coral species distributions reflects the pattern of the Indo-Pacific (Veron 1985) and has been attributed to long generation times and Pleistocene collapses in reef communities (Potts 1984).

The most notable exceptions to the above generalizations are Bermuda, the Flower Gardens, and, particularly, Brazil. The first contains a depauperate hermatypic scleractinian fauna, presumably, due to its high latitudinal position (32° N) and great distance (1700km) from the remainder of the Western Atlantic Province. The Flower Gardens (27°55'N) also possess a restricted scleractinian fauna due to their isolation and the cool temperatures experienced (Bright et al.

1984). The Brazilian area, which is also at a relatively high latitudinal position (23° S), is separated from the rest of the province by the Amazon-Orinoco system and has been classified as a separate subprovince due to the absence of many Caribbean-Western Atlantic species and the presence of endemic Brazilian species (Glynn 1973).

Although widely distributed, the relative abundances of species differ greatly from site to site. Certain of these differences are readily explainable in terms of differences in the ambient environments (e.g. the high abundance of Siderastrea siderea at cold Venezuelan sites, the high abundance of Montastrea cavernosa at Colombian sites with high sedimentation, and the general exclusion of Acropora species from cold localities), others, however, are not and may reflect stochastic processes.

The discussion of the following quantitative trends should be prefaced with the caveat that our census data are limited in extent and there is a dearth of quantitative data to draw from in the Western Atlantic reef literature. Unfortunately, it is unlikely that this situation can be remedied in the near future as many Western Atlantic reefs continue to manifest high algal/coral ratios following the mass mortality of the urchin Diadema. Nevertheless, it may be profitable to examine certain hypotheses relating coral reef community structure to physical-chemical or biotic parameters in light of the currently available data.

Porter (1974) suggested, based on his data from Panama, that coral diversity on Caribbean reefs may be positively correlated with coral abundance. Liddell & Ohlhorst (1987) found a significant inverse relationship between coral diversity and abundance on the West Fore Reef at Jamaica. However, an expanded data set consisting of 50 sites from Western Atlantic localities (Fig. 2) reveals no significant correlation between coral diversity and coral abundance.

Several authors (e.g. Porter 1972, Goldberg 1973, and Fricke & Meischner 1985) have documented rapid declines in coral diversity below 30m, leaving the impression that deeper-water faunas are highly impoverished. If suitable hard substrata is available for colonization, however, coral diversity may remain as high as or higher than shallow sites to appreciably greater depths than 30m (e.g. Jamaica data, Fig. 3). Furthermore, total community diversity may remain high to depths of over 100m (Liddell & Ohlhorst 1988).

Highsmith (1980), Johannes et al. (1983), Littler & Littler (1985), Maragos et al. (1985), and others have related trends in the abundance of groups such as algae and boring sponges to low temperatures and/or high nutrient levels which may be influenced by latitude, upwelling, stream run-off, or pollution. As such, a greater abundance of algae and, possibly, boring sponges might be predicted from the Colombian and Venezuelan sites, which experience cold (down to 18°C) upwelling (Antonius 1972, 1980). This, however, is not reflected by the present data (Table 2). Relatively low coral abundances at these sites are a consequence of low total living cover (due to a combination of low temperatures and high sedimentation), not increased boring sponge or algal abundances. Although data on noncrustose algal or boring sponge abundances are not given by Bright et al. (1984) for the Flower Gardens, coral abundance (40% of the substratum) is similar to the majority of Western Atlantic sites (Table 2), despite the cold winter temperatures (18°C) experienced. Finally, Bunt et al. (1981) found no change in coral abundance (admittedly, very low at their sites) across a 9° latitudinal range in the Bahamian region. The apparent incongruities between theory and this limited data set suggests potential areas for future study.

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