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A Tale of Germs, Storms, and Bombs: Geomorphology and Coral Assemblage Structure at Vieques (Puerto Rico) Compared to St. Croix (U.S. Virgin Islands)

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ABSTRACT

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The former U.S. Navy range at Vieques Island (Puerto Rico, United States) is now the largest national wildlife refuge in the Caribbean. We investigated the geomorphology and benthic assemblage structure to understand the status of the coral reefs. Coral assemblages were quantified at 24 sites at Vieques and at 6 sites at St. Croix, U.S. Virgin Islands. These sites were chosen to represent the major zones of reef geomorphology. Sites consisted of two or three 21-m-long photo-quadrat belt transects. The results revealed surprisingly little differentiation in the coral assemblages within and between reefs of comparable geomorphological and oceanographic setting at Vieques and St. Croix. At Vieques, the *Acropora palmata* zone was almost completely lost, and it was severely reduced at St. Croix, presumably primarily due to diseases and hurricane impacts since the 1970s. Subtle, but nonsignificant, differences with respect to the nature of the shelf margin (north adjacent to the bank, south adjacent to the open sea) and depth zone were observed at Vieques. At St. Croix, benthic assemblages differed more between depth zones but not between north and south. Effects of natural disturbances were severe at Vieques, outweighing impacts of past military activity—which were present but not quantitatively discernible at our scale of sampling. Germs and storms, rather than bombs (and associated naval activities), primarily seem to have taken the worst toll on corals at both Vieques and St. Croix.

ADDITIONAL INDEX WORDS: *Coral reefs, Caribbean, Acropora, degradation, disease, bombing range, navy.*

INTRODUCTION

Vieques is one of the lesser-known and smaller sister islands of Puerto Rico, and relatively little information exists about its coral reefs. For about six decades, much of its land area was used as a U.S. Navy training facility that was closed to the public, making little scientific research possible. In 2003, authority was transferred to the U.S. Fish and Wildlife Service and Vieques has gained renewed scientific significance as the largest national wildlife refuge in the Caribbean.

Although much effort has gone into reef mapping (HERNANDEZ-CRUZ, PURKIS, and RIEGL, 2006; KENDALL and ESCHELBACH, 2006; MONACO, CHRISTENSEN, and ROHMANN, 2001), little is known about reef geomorphology and constituent coral assemblages. The long military use of Vieques creates an interesting case study. On the negative side, the potential for damage by live-fire exercises has long been recognized (ANTONIUS and WEINER, 1982; DEPARTMENT OF NAVY STAFF, 1980, 1986; PORTER, 2000a, 2000b; ROGERS, CINTRON, and GOENAGA, 1978). On the positive side, Vieques is one of the few areas in the Caribbean that has had limited

development activities and development-related runoff and pollution. Much of the area used by the navy remained free of buildings, and impacts were largely limited to construction/maintenance of ammunition dumps, live-fire exercises, and relatively small-scale land clearing for military activities. Because of the restricted use of the land during the navy's tenure, most anthropogenic impacts that are usually implicated throughout the Caribbean as causing reef decline (papers in GINSBURG, 1993) were absent in Vieques. Thus, the opportunity existed to investigate a reef system with fewer and/or different (*i.e.*, navy) human impacts than on a neighboring island. St. Croix is close to Vieques, is very well studied, and has reefs partly protected as a national park. Natural disturbances have taken a high toll, particularly among the acroporids, previously dominant in the system (BYTHELL *et al.*, 1989; BYTHELL, BYTHELL, and GLADFELTER, 1993; HUBBARD *et al.*, 1991; ROGERS, 1993a, 1993b; ROGERS, MILLER, and WAARA, 2000). The comparison between the two islands helps shed light on the degree to which coral diseases, hurricanes, and bombs contributed to the overall degradation.

The aims of this study were to (1) describe the geomorphology of the reefs; (2) investigate the degree to which zonation and community differentiation can be observed through establishing a baseline on coverage, abundance, diversity, and assemblage structure of scleractinian, millepor-

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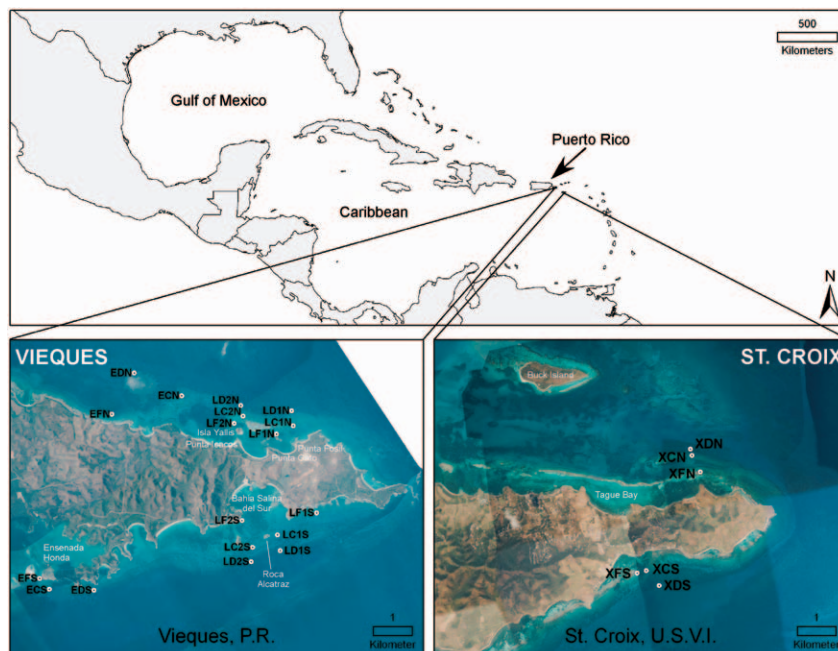


Figure 1. Study site locations on St. Croix and Vieques, with reef morphology profiles for Vieques (bottom left and right) sites. The extent of the former bombing range on Vieques (LIA = live impact area) and maneuver zone (EMA = external maneuver area) are visible by site codes; place names mentioned in the text are shown.

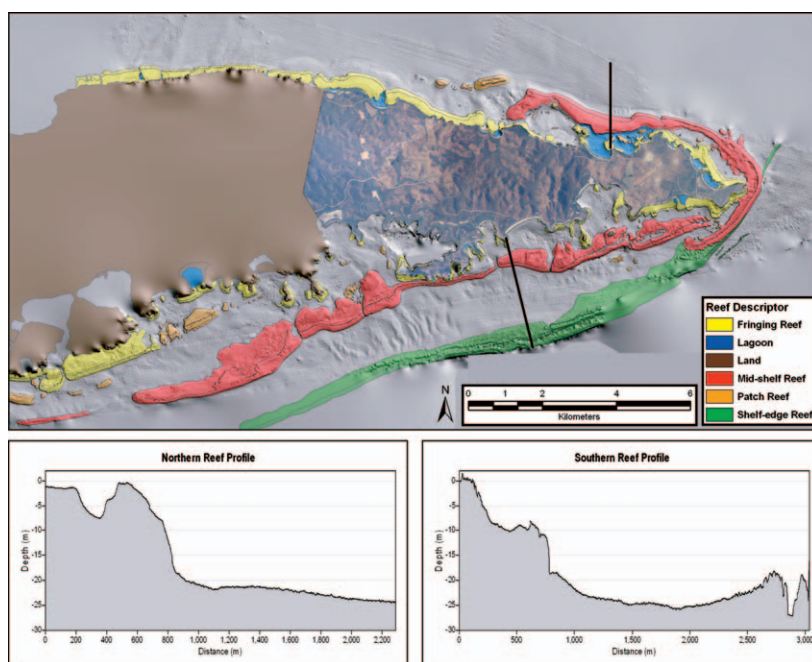


Figure 2. Bathymetry around Vieques (depth scale in meters) based on U.S. Navy and U.S. Geological Survey bathymetric lidar with selected profiles across the upper shelf and coral reefs. Easily discerned along the depth profiles are the fringing reefs, midshelf reefs, and shelf-edge reefs. The northern reef profile shows a tall *Acropora palmata*-built barrier reef. This structure is unique on the north coast along only a relatively short distance. The southern reef profile clearly shows the fringing reef, the midshelf reef, and the shelf-edge reef, all in increasing depth.

Table 1. Summary of sampling locations at Vieques and St. Croix.¹

	Code	Latitude	Longitude	Inside Bombing Range?	Side of Island	Depth Group
Vieques	LD1N	18°09.168199	65°17.733202	Yes	N	Deep
Vieques	LC1N	18°08.957766	65°17.704196	Yes	N	Medium
Vieques	LF1N	18°08.837498	65°17.948601	Yes	N	Shallow
Vieques	LD2N	18°09.232324	65°18.475878	Yes	N	Deep
Vieques	LC2N	18°09.087567	65°18.441723	Yes	N	Medium
Vieques	LF2N	18°08.980166	65°18.571752	Yes	N	Shallow
Vieques	EDN	18°09.669591	65°20.040342	No	N	Deep
Vieques	ECN	18°09.357355	65°19.341409	No	N	Medium
Vieques	EFN	18°09.087831	65°20.359255	No	N	Shallow
Vieques	LD1S	18°07.210828	65°17.874281	Yes	S	Deep
Vieques	LC1S	18°07.428724	65°17.914429	Yes	S	Medium
Vieques	LF1S	18°07.744722	65°17.348118	Yes	S	Shallow
Vieques	LD2S	18°07.050816	65°18.296741	Yes	S	Deep
Vieques	LC2S	18°07.251221	65°18.279740	Yes	S	Medium
Vieques	LF2S	18°07.626501	65°18.437000	Yes	S	Shallow
Vieques	EDS	18°06.621353	65°20.590502	No	S	Deep
Vieques	ECS	18°06.627893	65°21.242698	No	S	Medium
Vieques	EFS	18°06.778455	65°21.387449	No	S	Shallow
St. Croix	XDN	17°46.219080	64°35.186682	N.A.	N	Deep
St. Croix	XCN	17°46.159494	64°35.172192	N.A.	N	Medium
St. Croix	XFN	17°45.921258	64°34.990350	N.A.	N	Shallow
St. Croix	XDS1	17°44.313582	64°35.650752	N.A.	S	Deep
St. Croix	XCS	17°44.421114	64°35.783874	N.A.	S	Medium
St. Croix	XFS1	17°44.454162	64°35.898336	N.A.	S	Shallow

¹ Latitude and longitude are given in degrees and decimal minutes.

id, and alcyonacean corals; and (3) compare the variability of assemblages of reef zones between Vieques and St. Croix to evaluate differences and natural and anthropogenic factors, which had obvious influence.

METHODS

Eighteen sites at Vieques and six sites at St. Croix (Figure 1) were established for evaluation of coral assemblage structure (Table 1). Sites were stratified by habitat and depth into (1) *shallow* (mostly ~5 m) reef areas close to reef crests on fringing reef or equivalent setting (six sites, 18 transects at Vieques; two sites, 6 transects at St. Croix), (2) *medium-deep* (mostly ~7 m) areas (crests of midshelf reefs; six sites, 18 transects at Vieques; two sites, 6 transects at St. Croix), and (3) *deep* (mostly ~15m) areas (slopes of midshelf reefs; six sites, 12 transects at Vieques; two sites, 4 transects at St. Croix). Site selection was stratified random and ignored the nonreef area. Sample sites were haphazardly chosen at suitable locations within the reefs zones that were identified after geomorphological analysis. Equal numbers of sites were placed in each habitat and depth zone at Vieques, which included 12 inside the former bombing range (live-impact area, or LIA) and 6 outside (in the eastern maneuver area, or EMA, where landing exercises, but no bombing, were conducted). We concentrated on fringing and midshelf reefs while neglecting the shelf-edge reef and many areas of sparsely coral-covered hardgrounds. This limitation prohibited a comprehensive characterization of the entire range of habitats in Vieques and St. Croix but served to define specific assemblages in the chosen zones of coral reef.

To assess coral assemblages, we modified the methodology

of JAAP *et al.* (2000) and ROGERS, MILLER, and WAARA (2000). Each shallow site consisted of three 20-m-long transects arranged in a starlike fashion; each deep site had two 20-m-long parallel transects. Stainless steel stakes were placed every 5 m along each transect. Overlapping photographs of a 30 m² (20 × 1.5 m) area were taken with a digital camera mounted on a 0.75-m² quadruped framer. Transect and photograph number was included on a slate to avoid loss of sequence. Images were analyzed using Coral Point Count with Excel Extension (CPCe; KOHLER, and GILL, 2006). The optimum number of projected random points on each image was calculated using LENTH's power and sample size calculator (<http://www.stat.uiowa.edu/~rlenth/Power/>). Twenty random points were found to be an adequate sample size. These data are henceforth referred to as "CPC data." While photos were taken underwater, scleractinian, milleporid, and alcyonacean corals were recorded to species, as were diseases or damage to the corals. This dataset is henceforth referred to as "in situ coral counts."

Both datasets were compiled as individual species-by-transects matrices. All quadrates were pooled by transect. Analyses of CPCe data were performed on one dataset consisting of individual transects and one of the transects pooled per site. To smooth differences between common and rarer species and variability in variance, data were transformed by their square root. We did not choose a stronger transformation (such as fourth root) since we wanted to primarily emphasize species with "midrange" frequency. A Bray-Curtis similarity was calculated between all site pairs based both on species abundances and on presence/absence as $S = 100 * [1 - \sum |y_{ik} - y_{jk}| / \sum (y_{ik} + y_{jk})]$ (where y_{ik} is the entry in row

i and column k , hence the abundance of the i -th species in the k -th sample). To detect groupings, we used agglomerative hierarchical cluster analysis and nonmetric multidimensional scaling (nMDS) (CLARKE and GORLEY, 2001; CLARKE and WARWICK, 2001; WARWICK and CLARKE 1993). Cluster analysis has advantages for delineating groups in a distinct assemblage setting, while nMDS is better when gradations between assemblages are expected (CLARKE and WARWICK, 2001). If both analyses provide consistent results, it is likely that they represent natural groupings. *A priori* groups (e.g., LIA/EMA, N/S) were tested against the null hypothesis of no differences in assemblage composition by one-way analysis of similarity (ANOSIM) (CLARKE and GREEN, 1988) built on a nonmetric permutation of the rank-similarity matrix, with no assumption of normality and tolerance of zero-value dominance. The global test provides a single output statistic (global R) which ranges from 0 to 1. When the $R = 1$ similarity within sites is greater than among sites, then $R = 0$ similarities within and among sites will be the same.

Ecological diversity was expressed using a variety of indices (MAGURRAN, 1988), because not every diversity index performs equally well under the given sample-size constraints and each index measures a distinct component of species diversity (MAGURRAN, 1988; PIELOU, 1975):

- (1) Margalef's species richness, $D = (S - 1)/\ln N$ (S = number of species, N = number of individuals), reflects more or less directly species richness.
- (2) Shannon-Wiener diversity index, $H' = -\sum p_i \ln p_i$, where $p_i = n_i/N$, (p_i = proportion of individuals in the i -th species), is biased toward rare species, more powerful with larger sample sizes, and sensitive to sample size.
- (3) Pielou's evenness measure for the Shannon-Wiener diversity index, $E = H'/H'_{\max} = H'/\ln S$, measures equitability of species distribution for Shannon-Wiener's index. It takes highest value when all species have the same abundance.
- (4) 1-Simpson's dominance index is a reliable and unbiased diversity index: $1 - \lambda'$, where $\lambda' = \sum(n_i(n_i - 1)/N(N - 1))$. It acts as an evenness index and takes the highest value when all species have the same abundance. It is an appropriate index for small samples.

Identification of corals was carried out either in the field for immediate recording of species presence/absence or from photographs for point counts, and the same criteria was used to identify the species on the photographs in the laboratory as were used in the field using HUMANN (1993). Data were evaluated in Primer 5 (CLARKE and GORLEY, 2001).

RESULTS

Geomorphology of Reefs of Vieques and St. Croix

Vieques is situated on the southern edge of the Puerto Rico-Hispaniola microplate, which is a block bounded to the north and the south by deep trenches resultant of the strike-slip and oblique subduction between the North American and the Caribbean plates. The Muertos Trough south of Vieques has a maximum depth of 5500 m. To the east, the Anegada passage is a right-lateral transtensional fault (VAN GESTEL

et al., 1999). Rocks on Vieques are continuations of similar strata on Puerto Rico. Three tectonic phases shaped these islands (VAN GESTEL *et al.*, 1999). From the Cretaceous to the Eocene, the Greater Antilles arc formed a subduction zone and a forearc basin was formed and filled in on the Puerto Rico Trench side. By the middle Oligocene to the early Pliocene, arc activity had ended and the Puerto Rico-Virgin Islands (PRVI) platform and a carbonate sedimentary structure covering much of the platform was formed. From the early Pliocene to the Holocene, the PRVI platform was tilted and Puerto Rico (and Vieques) uplifted. This led to the carbonate cover (the PRVI platform) being eroded and leading to the outcropping of arc basement. The rocks on Vieques are thus both carbonate and arc basement, which has implications for modern reef growth.

St. Croix is a largely sedimentary island separated from Puerto Rico and the Greater Antilles arc by the Virgin Island basin, the Anegada passage, and the St. Croix basin. It was possibly rifted away from Puerto Rico by left-lateral faulting and was initially part of the Virgin Islands platform. Rock strata cropping out on St. Croix are Cretaceous-age siliciclastic and intrusive rocks of the Mt. Eagle group on either end of the island, and a Tertiary limestone basin consisting of the Jealousy (Early-Middle Miocene), Kingshill (Miocene/Pliocene), and Blessing (Pliocene) formations in its central basin (GILL *et al.*, 1985). The Jealousy Formation was deposited in 600–800 m of water. The early Miocene Kingshill Formation was deposited in a graben system. Continued shoaling led to the deposition of the Blessing Formation in the Pliocene, which also includes coral reefs as typical shallow water elements (GILL and HUBBARD, 1985; GILL *et al.*, 1985).

From the history and geomorphological setting, a number of constraints arise for reef building at Vieques and St. Croix:

- Both are high islands partly made up of arc basement rocks and siliciclastics, which weather well and form thick soil. Therefore, land runoff can be an important control on reef building, and fringing reefs are interrupted along major drainage lines.
- The southern part of Vieques faces the Muertos Trench, while the northern part faces the platform of the Hispaniola-Puerto Rico plate, which is a wide expanse of shallow water. This leads to a different oceanographic setting and therefore different environmental conditions for reef development. Corals grow in greater density on the southern coast.
- St. Croix has a wider southern shelf. The northern shelf is broader at the east end than to the west, and the fringing reefs abut a bank, which rises toward Buck Island.
- The differing bathymetry on the northern and southern coasts of Vieques and St. Croix would also have resulted in different reef initiation histories and structures during sea-level rises after lowstands, particularly in deeper water (HUBBARD, BURKE, and GILL, 1985; HUBBARD *et al.*, 2005). The reefs on the southern side of Vieques would have initiated earlier, while the platform to the north was still barely flooded and not yet suitable for reef development.

Since the beginning of the Holocene transgression, sea-level rise appears to have been fairly uniform throughout the Caribbean basin (HUBBARD *et al.*, 2005; TOSCANO and MAC-

INTYRE, 2003), but some authors suggest it to have been stepped in time (BLANCHON and JONES, 1995). Rising sea level had a powerful influence on reef geometries by eroding wide platforms into the Pleistocene rocks (BLANCHON and JONES, 1995; GEISTER, 1984) and by causing reef backstepping (HUBBARD *et al.*, 1997). Many Caribbean reefs exhibit a comparable morphology, which can, at least partly, be correlated to sea-level episodes (GEISTER, 1984). However, since tectonic history exerts control over sea level, the different tectonic history of Vieques and St. Croix has indeed led to differences in large-scale reef profiles (HUBBARD, personal communication). As a gross simplification, the following rough zonation can be generalized (Figure 2):

- On outer slopes, a drop-off into the surrounding basin is found between 20 and 30 m. This is often the locus of a shelf-edge reef (green in Figure 2).
- This is followed shoreward by a platform terminating in a midshelf structure (sometimes a scarp—red in Figure 2).
- Further shoreward, there is an upper planation platform that terminates in a fringing reef or the modern sea-level cliff (yellow in Figure 2).

Sea-level-driven morphology led to the development of three distinct reef types and zones: shelf-edge, midshelf, and fringing (Figure 2). During early Holocene sea-level rise, a shelf-edge reef developed on the outer shelf edge (BLANCHON and JONES, 1997; HUBBARD, BURKE, and GILL, 1985). This reef did not catch up to the rising ocean surface (HUBBARD, BURKE, and GILL, 1985). Debate exists as to the exact cause of the reef drowning, whether mediated by disturbance events like hurricanes, rapid sea-level rise, or inimical water conditions forming in the lagoon (BLANCHON and JONES, 1997; HUBBARD, BURKE, and GILL, 1985; NEUMANN and MACINTYRE, 1985). In Vieques, this shelf-edge structure is only found on the south coast, adjacent to the drop-off into the Virgin Islands basin. On the north coast, which faces the flat top of the platform, no shelf-edge that could have served as locus for reef development is found. At the eastern section of St. Croix, shelf-edge structures on the northern side are confined to offshore Buck Island, but the situation is different further west, where the shelf is narrower. Inshore of the shelf-edge reef at Vieques, a series of more or less well-connected reef patches can be found (for the situation in St. Croix, see HUBBARD *et al.*, 2005). A midshelf structure usually colonized by dense coral growth, and active carbonate accretion is frequently found between the shelf edge and the present shoreline. Thickness or even presence of carbonate accretion is unknown, but this is a possibly younger structure than the shelf-edge reef. It may be of similar age as the fringing reef and either could relate to a temporary slowing in Holocene sea-level rise (BLANCHON and JONES, 1995) or may be related to Pleistocene topography—but we have no reliable information. HUBBARD *et al.* (1997) observed similar reef backstepping in SW Puerto Rico. The present day shoreline has in many areas a fringing reef, which is discontinuous and generally best developed around headlands, where runoff and sedimentation are lowest. This reef is not always a well-developed carbonate structure, but some level of accretion is usually present that covers the bedrock. A fringing reef at

Bahia Salina del Sur on Vieques was drilled and studied in detail by MACINTYRE, RAYMOND, and STUCKENRATH (1983).

Between the reefs, wide, gently sloping platforms are found. The lower platform is covered by a carbonate sand layer, presumably derived from the shelf-edge and shallow bank reefs and by sediment production from green algae (*Halimeda* sp., *Penicillus* sp.) on the sand. The upper platform is only partly covered by sand. Where it is exposed, the bedrock areas are usually covered by variably dense growth of reef-associated organisms and some active carbonate accretion can be found. Some localized framework patches also occur.

Vieques and St. Croix: Corals and Benthic Categories in the Transects

The five most abundant stony corals (scleractinia and milleporids) at Vieques were (Figure 3, top panel) (1) *Porites porites* ($N = 1314$), (2) *Millepora* spp. ($N = 1126$), (3) *Montastraea annularis* ($N = 1034$), (4) *P. astreoides* ($N = 904$), and (5) *Siderastrea siderea* ($N = 573$). The five most frequent CPCe-counted benthic categories at Vieques were (Figure 3A) (1) sand, pavement, rubble ($57.2 \pm 21.3\%$); (2) macroalgae ($14.18 \pm 11.8\%$); (3) alcyonaceans ($8.21 \pm 6.05\%$); (4) stony corals ($8.21 \pm 6.05\%$); and (5) dead corals with algae ($2.2 \pm 2.7\%$). At Vieques, 61.5% of all encountered stony corals were the five dominant species. *Acropora palmata* was not among them. At St. Croix, the five most abundant stony coral species were (Figure 3, lower panel) (1) *S. siderea* ($N = 480$), (2) *S. radians* ($N = 479$), (3) *Diploria strigosa* ($N = 474$), (4) *Agaricia agaricites* ($N = 362$), (5) *P. astreoides* ($N = 184$). They made up 68.8% of all stony corals. For St. Croix and similar to Vieques, live acroporids were not among the most common species. The five most abundant benthic categories at St. Croix were (Figure 4) (1) sand, pavement, rubble ($54.9 \pm 12.6\%$); (2) macroalgae ($12.1 \pm 9.2\%$); (3) stony corals ($4.7 \pm 2.3\%$); (4) dead corals with algae ($2.2 \pm 2.7\%$); and (5) alcyonaceans ($1.9 \pm 2.02\%$). Coral diseases were found on $1.5 \pm 6.0\%$ of all stony corals at St. Croix, while they were found at Vieques on $0.6 \pm 2.3\%$. At St. Croix, stony corals covered more space than alcyonaceans, with the opposite at Vieques (Figure 4). At both St. Croix and Vieques, macroalgae were the most frequent living benthos (Figure 4).

Vieques and St. Croix: Different Assemblages at Different Depths?

Classification and ordination of *in situ* coral counts and CPCe data (Figures 5–7) showed a relatively homogeneous assemblage at both Vieques and St. Croix. Within-reef zonation was clearer at St. Croix than Vieques. A clearer depth zonation was obtained from the *in situ* coral counts (scleractinian presence/absence only) than from the CPCe data, which included all benthic categories (Figures 5–7). In the Vieques nMDS (Figure 5), a superposition of general zone/depth setting (“shallow” = 5 m, “medium” = 7 m, “deep” = 15 m) showed within-zone similarity based on *in situ* coral counts (Figure 5C) but ANOSIM showed no significant differences (global $R = 0.11$, $p > 0.05$). Figures 5C and 5D show that southern shallow sites did form a cluster that was set apart from the other sites. Also, some northern medium sites

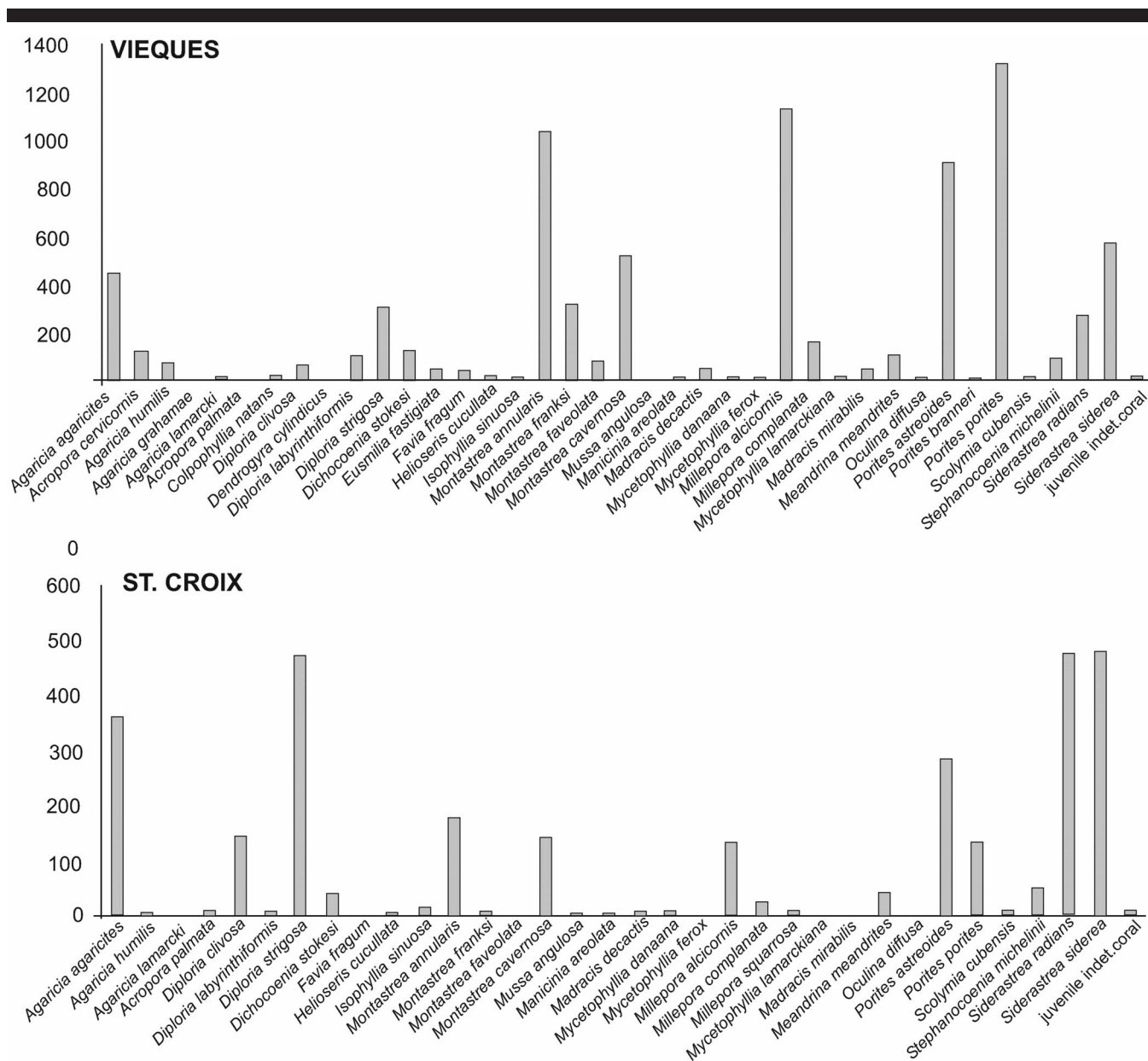


Figure 3. Abundance of coral species in CPCe data from Vieques and St. Croix.

formed a well-defined cluster, but most northern and southern shallow and medium sites formed an unresolved cluster in the center of the graph. Therefore, differences in the groupings were not significant (ANOSIM: $R = 0.17$, $p > 0.05$). While some depth gradient undoubtedly was present, it was confounded with a gradient defined by transect location on the island, *i.e.*, north vs. south. The diversity indices based on *in situ* coral counts did not differ significantly along a depth gradient, but some patterns were visible (Table 2). Shallowest sites had both the lowest number and the lowest diversity of stony corals. A Kruskal-Wallis test showed significant difference in number of species (S), Margalef's index

(d), and 1-Simpson's λ between depth groups but not in the other diversity measures (Table 2).

At St. Croix, classification and ordination of *in situ* coral counts revealed one distinct cluster in each reef zone, suggesting distinct assemblages (Figures 6A–H). Between-group dissimilarity was higher between medium and deep than between medium and shallow sites, with significant differences (ANOSIM: $R = 0.54$, $p = 0.001$). CPCe data (Figures 6E–H) suggested dissimilarity between medium and shallow sites, with significant differences (ANOSIM: $R = 0.42$, $p = 0.001$). Medium sites had highest stony coral diversity (Table 2) and number of species. A Kruskal-Wallis test showed significant

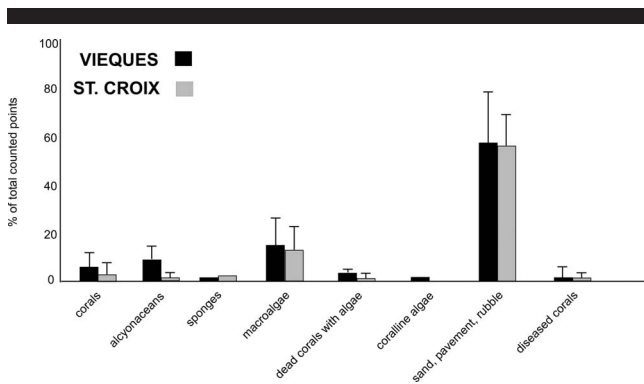


Figure 4. Mean relative frequency (\pm SD) of benthic categories in all CPCe data from Vieques and St. Croix.

differences in number of species, Margalef's index, and the Shannon index, as well as $1 - \lambda$ (Table 2).

CPCe data first pooled per site and then subjected to ordination suggested little differentiation into depth groups with no clear clusters formed. The outliers in Figure 7A are both sites from Vieques. LC2N, the shallow outlier, was characterized by an unusually high abundance of *Ac. cervicornis*. The deep outlier, LD1S, was marked by an unusually high abundance of *Madracis decactis* and *Mycetophyllia ferox*.

Bubble plots of the relative abundance of stony coral species derived from *in situ* data superimposed as scaled circles on the corresponding nMDS (Figure 8) suggested that *Millepora* spp. was the most frequently occurring stony coral at shallow sites. *P. porites*, *P. astreoides*, *S. siderea*, and *S. radians* were most frequent at medium depths. *Mo. annularis* was common in deep and shallow sites, while *Mo. cavernosa* and *Mo. franksi* were most common only in deep sites. *Ag. agaricites* and *D. strigosa* occurred in all three depths. *Ac. cervicornis* was more common than *Ac. palmata* ($N = 2$). At shallow site LC2N2, *Ac. cervicornis* was found in unusually high abundance ($N = 60$). Many dead *Ac. palmata* were encountered on the fringing reef of Roca Alcatraz and in Bahia Salina del Sur (Figure 1). Both *Acropora* spp. were primarily encountered at shallow sites (Figure 8). The bubble plots suggested a stony coral assemblage dominated by *Millepora* in the shallow; *Porites*, *Diploria*, and *Siderastrea* in medium; and *Montastraea* in the deep areas.

Bubble plots of Vieques benthic categories indicated no relationship of either zone/depth or site with the amount of bare substratum (sand, pavement, rubble; Figure 9). Highest-living stony coral cover was found at medium sites. Alcyonacean cover was nearly uniform across depth, but some shallow sites had very few alcyonaceans (LC1N1, LC1N2, LC1N3, LC2N1, LF1N2, LF1N1). Macroalgae were more frequent at shallow and medium sites and were more abundant at the northern sites.

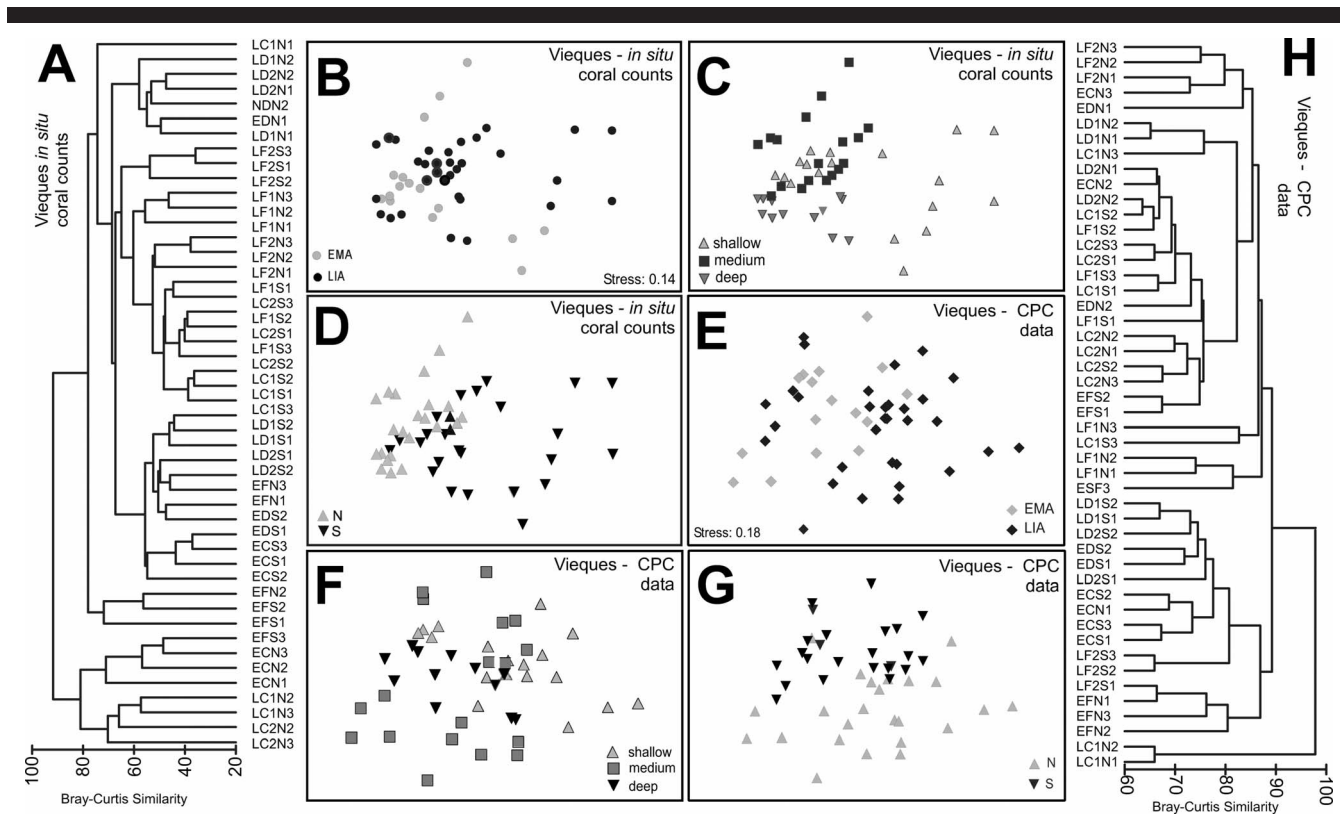


Figure 5. (A) Classification of *in situ* coral counts and CPCe data at Vieques. (A,H) Dendrograms corresponding to the nMDS plots. (B,E) Ordination of sites coded by position inside or outside bombing range (C,F) have the same ordination with sites coded by depth range (D,G), which have the same ordination with sites coded by their N-S position on island. In site codes, F = shallow, C = medium, D = deep, S = south, and N = north.

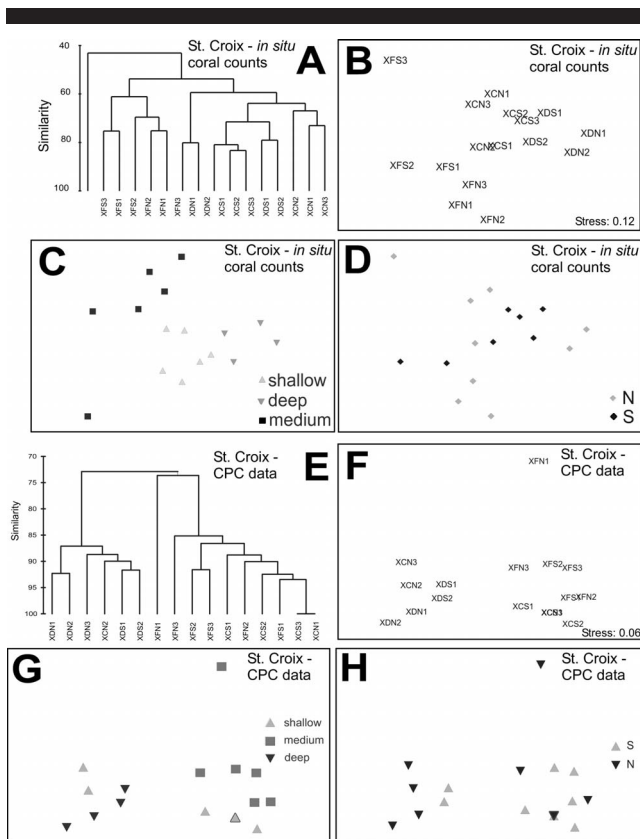


Figure 6. Classification and ordination of *in situ* coral counts and CPCe data at St. Croix. (A,E) Dendrograms correspond to the nMDS plots. (B, F) Ordination of sites (C,G) have the same ordination with sites coded by depth range (D,H), which have the same ordination with sites coded by their N-S position on island.

Coralline algae were most abundant at medium depths. Bleached corals were only found at medium sites, while diseased corals were found at medium and deep sites.

Bubble plots of St. Croix showed the five most common

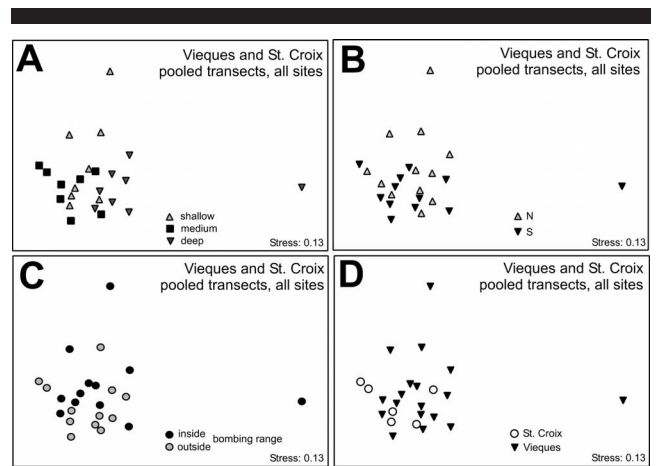


Figure 7. Ordination of CPCe data of transects pooled per site. All sites are from Vieques and St. Croix. (A) Depth zone, (B) differentiation N-S, (C) situation relative to bombing range, (D) identification of sites on St. Croix and Vieques.

stony corals occurring at all sites with no N-S trend but some depth zonation (Figure 10). In particular, *S. radians* occurred more frequently at medium sites. *Ag. agaricites* was more common at deep sites, while *S. siderea*, *P. astreoides*, and *D. strigosa* did not show any preferred depth distribution. Overall, depth zonation at St. Croix was similar to Vieques. Bubble plots of benthic categories showed bare substratum (sand, pavement, rubble) to be abundant at all depths. Stony corals were most abundant at medium sites, while alcyonaceans were more abundant at deep sites (Figure 11).

Vieques and St. Croix: Differences between the North and the South Coasts?

Neither at Vieques nor at St. Croix were differences found among benthic assemblages at the north and south coasts (Figures 6D, 6G; Vieques: ANOSIM global $R = 0.019$; St. Croix: global $R = 0.186$; $p > 0.05$). Also, Figure 7B shows an

Table 2. Summary of diversity statistics for Vieques and St. Croix sites.¹

	Shallow	Medium	Deep	K-W	All N	All S	U	LIA	EMA	U
VIEQUES										
S	13 ± 6	15 ± 4	12 ± 3	0.007*	13 ± 4	14 ± 5	0.002*	14 ± 4	13 ± 6	0.096
N	139 ± 122	197 ± 104	178 ± 5	0.25	132 ± 81	212 ± 125	0.001*	191 ± 111	133 ± 107	0.238
Margalef	2.45 ± 0.93	2.7 ± 0.7	2.13 ± 0.53	0.002*	2.42 ± 0.84	2.55 ± 0.75	0.017*	2.51 ± 0.65	2.43 ± 1.03	0.562
Evenness	0.75 ± 0.14	0.7 ± 0.08	0.72 ± 0.11	0.99	0.76 ± 0.12	0.74 ± 0.09	0.236	0.75 ± 0.09	0.74 ± 0.14	0.563
Shannon	1.81 ± 0.52	2.06 ± 0.35	1.76 ± 0.37	0.089	1.86 ± 0.48	1.95 ± 0.36	0.012*	1.96 ± 0.30	1.79 ± 0.60	0.056
1-Simpson	0.74 ± 1.69	0.82 ± 0.07	0.76 ± 0.10	0.034*	0.77 ± 0.14	0.79 ± 0.09	0.020*	0.80 ± 0.08	0.74 ± 0.17	0.080
ST. CROIX										
S	12 ± 1	18 ± 3	12 ± 3	0.026*	15 ± 4	12 ± 3	0.15			
N	140 ± 39	224 ± 94	220 ± 72	0.09	196 ± 73	186 ± 82	0.6			
Margalef	2.24 ± 0.12	3.16 ± 0.35	2.07 ± 0.64	0.031*	2.63 ± 0.59	2.18 ± 0.57	0.11			
Evenness	0.79 ± 0.04	0.82 ± 0.02	0.71 ± 0.10	0.072	0.79 ± 0.05	0.75 ± 0.10	0.67			
Shannon	1.98 ± 0.12	2.38 ± 0.11	1.78 ± 0.37	0.013*	2.12 ± 0.23	1.89 ± 0.39	0.17			
1-Simpson	0.83 ± 0.03	0.88 ± 0.01	0.76 ± 0.09	0.008*	0.84 ± 0.03	0.79 ± 0.09	0.4			

¹ Differences among shallow, medium, and deep sites were evaluated by Kruskal-Wallis tests, with significance given in column K-W. North (N) versus south (S) and live impact area (LIA = bombing range) versus external maneuver area (EMA) were tested with Mann-Whitney U tests; the significance levels are given in column U. Significance is indicated by *.

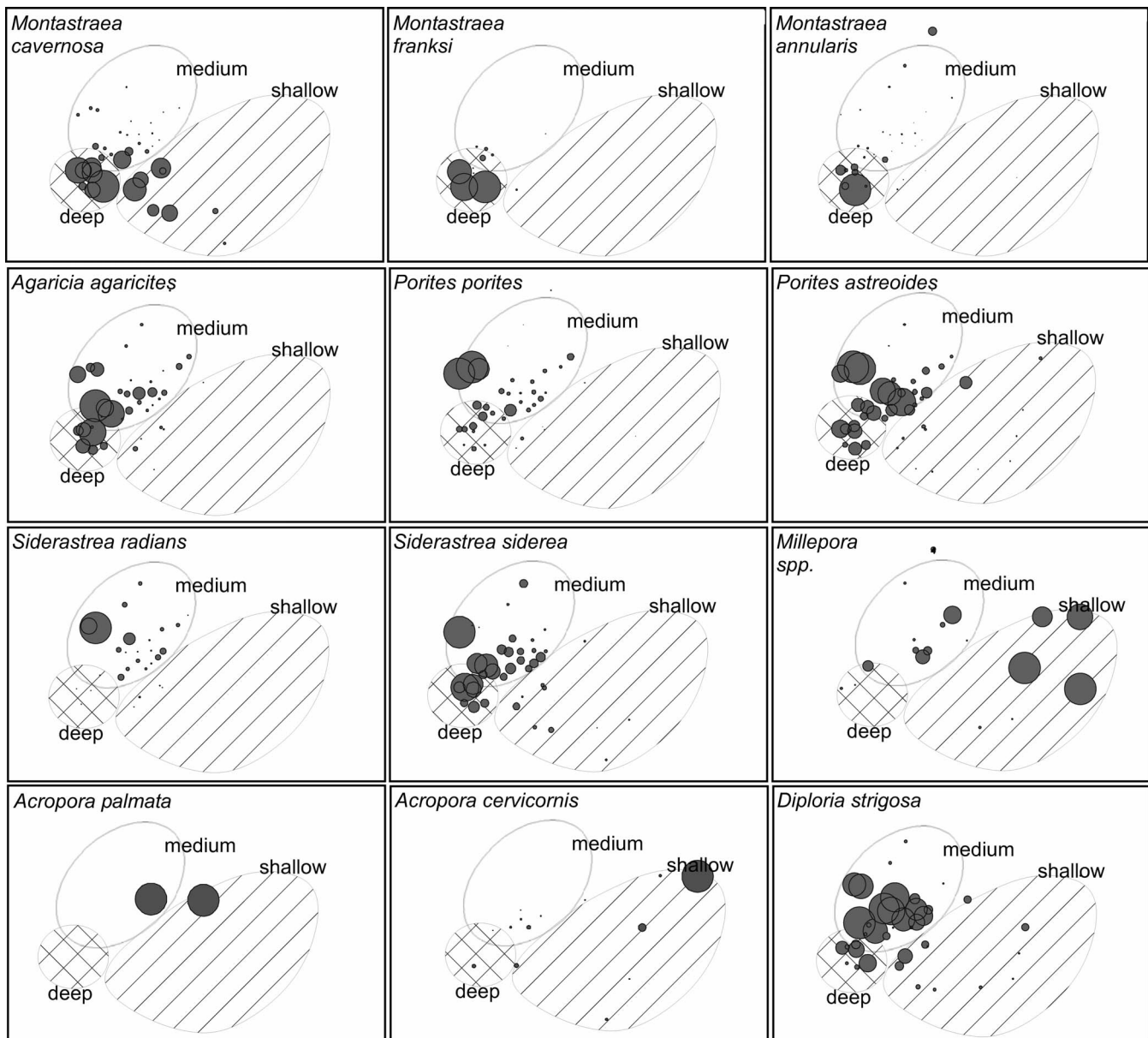


Figure 8. Bubble plots of stony coral frequency at Vieques. Ordination maps are same as those in Figure 5 but superimposed with bubbles of size relative to coral frequency.

absence of a clear N–S differentiation. Total benthic diversity differed between north and south at Vieques (Table 2). At St. Croix, no N–S differences in stony diversity (Table 2) or coral frequency were found in either *in situ* coral counts or CPCe data (ANOSIM: $R = 0.036$, global $R = 0.101$, $p = 0.101$).

Vieques: Differences between Inside and Outside the Bombing Range?

Neither *in situ* coral counts (ANOSIM: global $R = 0.08$, $p = 0.11$) nor CPCe data (global $R = 0.035$, $p = 0.25$) suggested differences of coral assemblages. The five most common stony

corals were widely distributed and found both inside and outside the bombing range. Diversity statistics based on *in situ* coral counts showed no differences between inside and outside the bombing range, confirmed by Mann-Whitney U-tests (Table 2). Also, in Figure 7C, the CPCe data of transects pooled per site suggest no difference.

Differences between Vieques and St. Croix?

Neither *in situ* coral count data nor CPCe data of all benthic categories from St. Croix and Vieques split in cluster analysis or nMDS. Also, ANOSIM showed no significant dif-

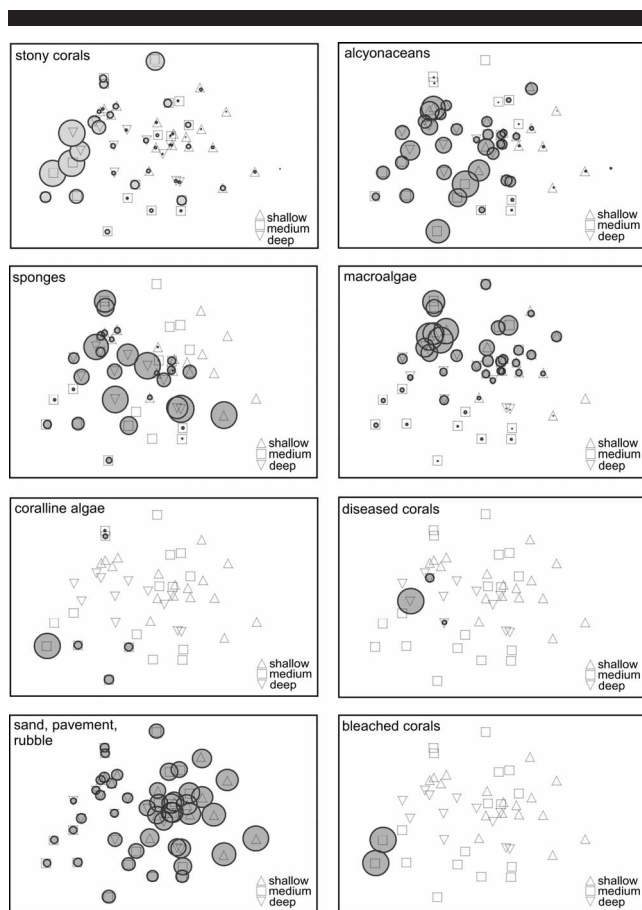


Figure 9. Bubble plots of benthic cover categories at Vieques, showing some degree of depth preferences. For size of bubble relative to cover, the depth code is superimposed, but size of depth icon is not related to any value.

ferences between Vieques and St. Croix (global $R = 0.068$, $p = 0.2$). CPCe data pooled per site also revealed no division of Vieques or St. Croix into separate clusters (Figure 7D). This suggests that, overall, coral assemblages at the sites at the two islands were similar in composition.

DISCUSSION

The most pronounced outcome of this study was the lack of differentiation within and between the coral communities of Vieques and St. Croix. The coral assemblages investigated in the 24 sites at Vieques and St. Croix were overall similar in composition and biotic coverage, although coral cover was slightly higher at Vieques (8% stony corals, 8% alcyonaceans) than at St. Croix (5% stony corals, 2% alcyonaceans).

According to the classical descriptions of Caribbean coral community structure (GOREAU, 1959) and previous reports (ANTONIUS and WEINER, 1982; MACINTYRE, RAYMOND, and STUCKENRATH, 1983), a very clear depth zonation should have been observable at both Vieques and St. Croix, defined most strongly by an *Ac. palmata* zone with the highest coral cover in the shallow sites. While some depth-dependent zo-

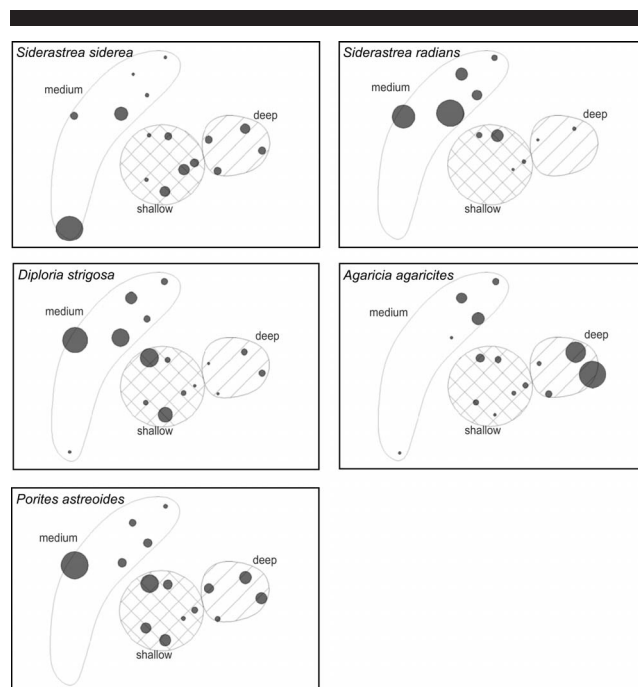


Figure 10. nMDS ordinations of *in situ* coral counts at St. Croix. The bubble size corresponds to the relative abundance of species at each site.

nation followed the geomorphology (Figure 2) at both islands, its appearance was greatly diminished by the absence of extensive live *Ac. palmata*, most notably at Vieques. Coral cover was not highest at shallow sites, but at medium sites, it was a direct consequence of *Ac. palmata* mortality. Only skeletons, stumps, and rubble were still abundant (Figure 12). Unless live, as well as dead, corals were taken into account, the classical Caribbean shallow *Ac. palmata* zone (GOREAU, 1959) was barely visible. Where present, the few living *Ac. palmata* and *Ac. cervicornis* were indeed mostly found at shallow sites, with *Ac. cervicornis* also occurring at low abundance at many medium and deeper sites. Previously dense *Ac. palmata* thickets had mostly been replaced by smaller, but similarly dense, frameworks of *Millepora* spp., now clearly dominant corals in the shallow (Figure 8), while the depth distribution of the other corals followed that known from the literature (BURNS, 1985; GOREAU, 1959; JAAP, 1984; KINZIE, 1973; LOYA, 1976; MOYER *et al.*, 2003). The notable absence of shallow *Acropora* emphasized that stony corals and alcyonaceans were more common away from the shallowest sites, which were dominated by coralline algae and macroalgae. Thus, the areas of previously highest coral cover in the *Ac. palmata* zone had become areas with lower coral cover than the deeper zones. At St. Croix, a depth zonation was more clearly visible in the data, but here the great decline of *Ac. palmata* in the shallow zone was dramatically visible.

Both at Vieques and at St. Croix, drastic changes had occurred since earlier studies, the most obvious being the loss of much of (St. Croix) or almost the entire (Vieques) *Ac. palmata* zone. ANTONIUS and WEINER (1982) were the last to illustrate dense stands of *Ac. palmata* in Bahia Salina del Sur

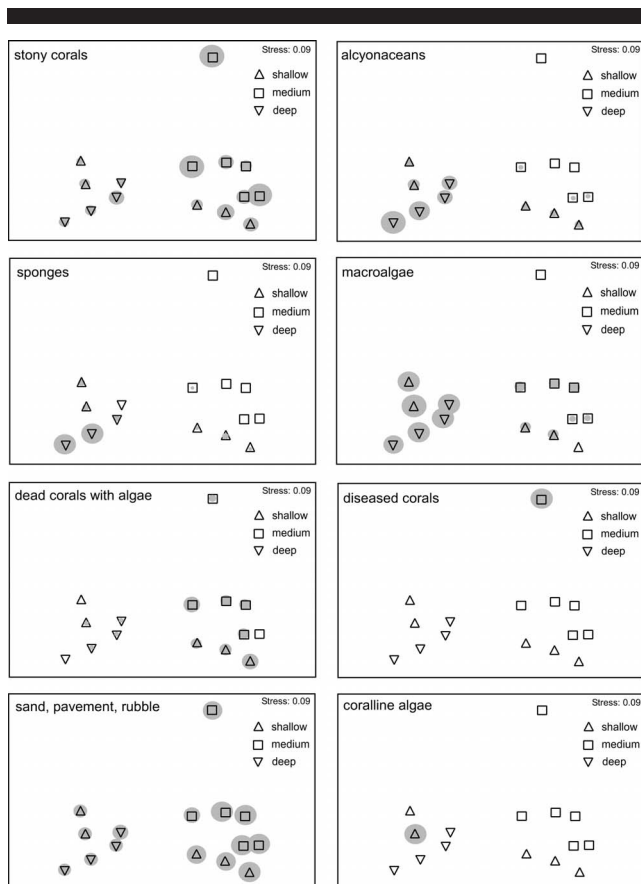


Figure 11. Bubble plots of benthic cover categories at St. Croix. Size of bubble signifies relative abundance of class and depth code is superimposed, but size of depth icon is not related to any value.

and around Roca Alcatraz at Vieques and noted that *Ac. palmata* was by far the most common coral in their study sites (more than 50% of all corals). HUBBARD *et al.* (2005) review and discuss the situation at St. Croix. In our study, *Ac. palmata* was a relatively rare species, with only vestigial stands or skeletons at Vieques and much-reduced abundance of live colonies at St. Croix. Our data show good agreement with the decline documented by many (see HUBBARD, GLADFELTER, and BYTHELL, 1993; HUBBARD *et al.*, 2005). The reasons for this decline are unclear at Vieques, but HERNANDEZ-CRUZ, PURKIS, and RIEGL (2006) constrained the timing of the decline via loss of optical signature of *Ac. palmata* in aerial images as between 1975 and 1985. This coincides with several regional-scale disturbances known to have affected reefs, such as the *Diadema* die-off (LESSIOS *et al.*, 1984), hurricanes, and the beginning of the white-band disease epizootic (GLADFELTER, 1982). ANTONIUS and WEINER (1982) observed white-band disease at Vieques, which also killed *Ac. palmata* in the wider Caribbean and the sites at St. Croix (ROGERS, 1993a, 1993b). Thus, *Ac. palmata* mortality at Vieques was likely due to one of the white diseases, and the low number of standing dead *Ac. palmata* frameworks is likely due to wave action by hurricanes (BLANCHON and JONES,

1997; ROGERS, 1993b; ROGERS, McLAIN, and TOBIAS, 1991). If corals died in the late 1970s, Tropical Storm Frederic (1979) and Hurricanes David (1979), Hugo (1989), Marilyn (1995), George (1998), and Lenny (1999) likely broke up the skeletons. Also, the situation at St. Croix, with live acroporids being relatively scarce although more conspicuous than at Vieques, suggests the same deadly combination of hurricanes and diseases (ARONSON, PRECHT, and MACINTYRE, 1998; GLADFELTER, 1982; HUBBARD *et al.*, 2005; ROGERS, 1993a).

Subtle differences existed in diversity between the north and the south coasts of Vieques but not at St. Croix. While southern Vieques is directly adjacent to the open oceanic conditions of the Caribbean Sea and near a trough, the north coast abuts the shallow bank waters of the Straits of Vieques with more turbid conditions and greater temperature variability. ROBERTS, WILSON, and LUGO-FERNANDEZ (1992) have shown the possible negative effects of shallow bank waters on reef development, and it is likely that the higher diversity on Vieques's south shore is in reaction to clearer and more temperate waters.

Were the reefs in Vieques, which were exposed to military bombing, overall in worse or better shape than the reefs on St. Croix? Military reef damage was studied in the 1970s and 1980s (DODGE, 1981; ROGERS, CINTRON, and GOENAGA, 1978). ANTONIUS and WEINER (1982) only reported localized damage. DODGE (1981) found similar extension rates of *Montastrea* between areas inside and outside the bombing range. DEPARTMENT OF NAVY (1980, 1986) reported military debris covering 0.4% of seafloor, less than 0.3% of reefs with damage, and only 2.24% of broken corals attributable to military activities (GEOMARINE, 2002). We observed unexploded bombs, casings, and ammunition shells around Roca Alcatraz, inside Bahia Salina del Sur, and near Punta Icacos, Punta Gato, Punta Fosil, and Isla Yallis. GEOMARINE (2002) estimated ordinance hits on 1,722 m² of coral reefs and 31,696 m² of sea grass. PORTER (2000a, 2000b) claimed significant damage by the navy. We found no differences in living benthic coral reef cover or composition of coral assemblages inside and outside the bombing range or in comparison to reefs investigated on St. Croix. This indicates not that zero impacts occurred but rather that natural disturbances appear to have altered the coral communities drastically, thus obscuring military impacts.

The reefs at St. Croix were subjected to similar environmental stressors (*i.e.*, hurricanes, *etc.*) but manmade impacts were more development and tourism related (*e.g.*, anchoring; ROGERS, 1993a) as compared to naval activities. Our study shows differences in living benthic cover and coral assemblage structure were nonsignificant between the two islands. The overall similarity of sites from Vieques and St. Croix suggests that the assemblage structure of both systems may be driven by comparable levels of disturbance. Our present knowledge does not allow us to judge whether natural or anthropogenic, or at least anthropogenically mediated, events disrupted the coral assemblages. But the fact that reefs at St. Croix were certainly not in a better condition than those at Vieques, and their condition comparable to that of many other reefs in the Caribbean (GINSBURG, 1993; LANG, 2003),

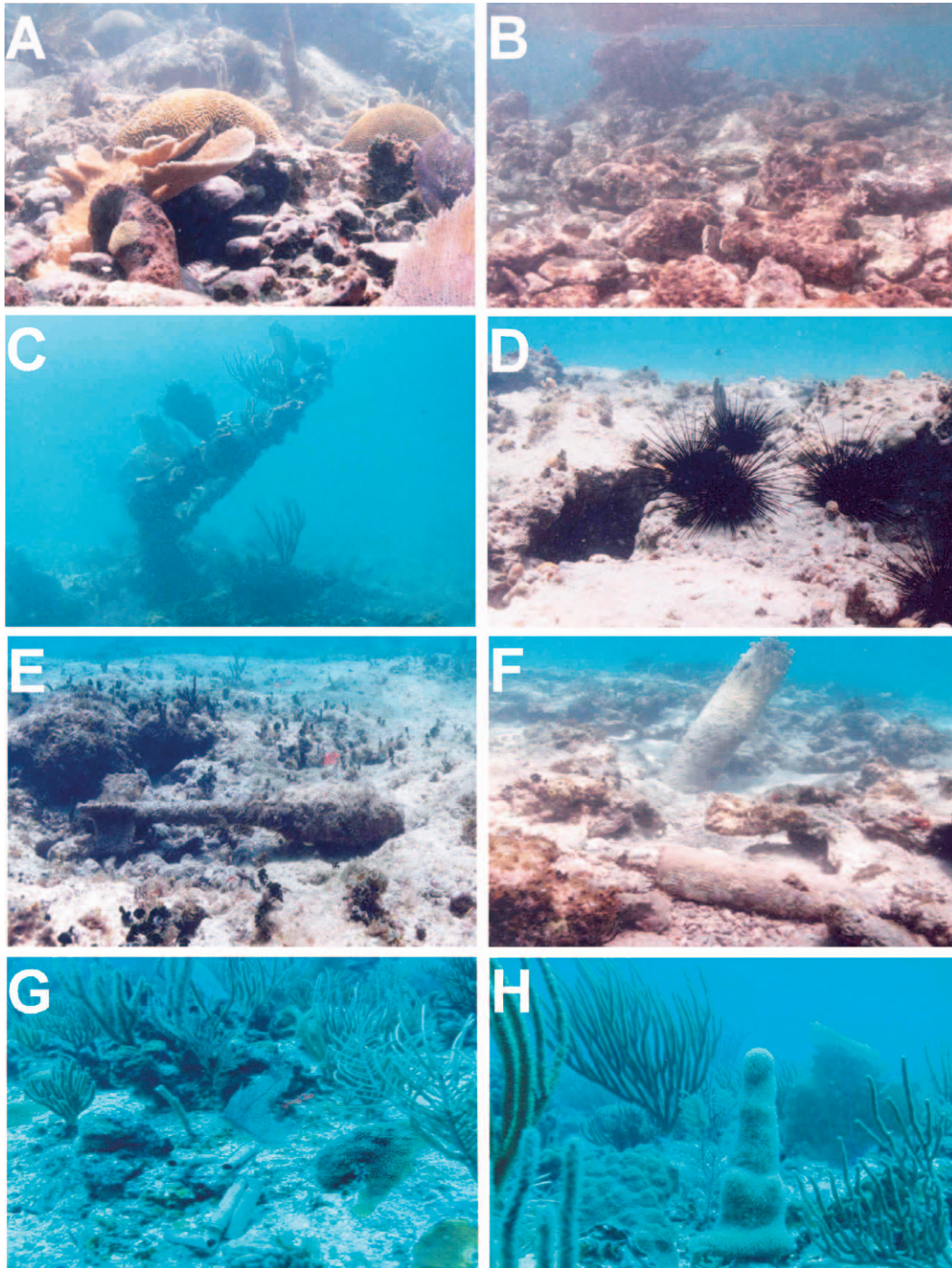


Figure 12. Images from Vieques: (A) Remnants and regeneration of formerly abundant *A. palmata*, which have all but disappeared from Vieques and suffered severe mortality at St. Croix. (B) Most frameworks are broken into rubble, but (C) some standing dead colonies remain. (D) *D. antillarum* were not rare in 2001 and 2005. (E, F) Military debris on reefs in the LIA. (G, H) The densest and most diverse coral growth of all sites was found on the southern, deep reefs of the Vieques LIA.

suggests that Caribbean-wide influences likely had the greater impact.

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