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GEOGRAPHIC VARIATION IN CLONAL STRUCTURE IN A REEF-BUILDING CARIBBEAN CORAL, *ACROPORA PALMATA*

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Abstract. Species that build the physical structure of ecosystems often reproduce clonally, both in terrestrial (e.g., grasses, trees) and marine (e.g., corals, seagrasses) environments. The degree of clonality may vary over a species' range in accordance with the relative success of sexual and asexual recruitment. High genotypic (clonal) diversity of structural species may promote the species diversity and resilience of ecosystems in the face of environmental extremes. Conversely, low genotypic diversity may indicate an asexual strategy to maintain resources and genetic variation during population decline. Here, we use microsatellite markers to assess geographic variation in clonality in the coral *Acropora palmata* sampled from 26 reefs in eight regions spanning its tropical western Atlantic range ($n = 751$). Caribbean-wide, the ratio ($\pm$SD) of genets (N_g) to sampled ramets (N) was 0.51 $\pm$ 0.28. Within reefs (30–70 m) and among reefs (10–100 km) within regions, clonal structure varied from being predominantly asexual (N_g/N approaching 0) to purely sexual ($N_g/N = 1$). However, two genetically isolated regions (western and eastern Caribbean) differed in clonal structure: genotypically depauperate populations ($N_g/N = 0.43 \pm 0.31$) with lower densities (0.13 $\pm$ 0.08 colonies/m^2) characterized the western region, while denser (0.30 $\pm$ 0.21 colonies/m^2), genotypically rich stands ($N_g/N = 0.64 \pm 0.17$) typified the eastern Caribbean. Genotypic richness (standardized to sample size; N_g/N) and genotypic diversity (G_o/G_e) were negatively related to colony density within each province ($r^2 = 0.49$–0.66, $P < 0.001$), indicating that dense stands have higher rates of asexual recruitment than less dense populations. Asexual recruitment was not correlated with large-scale disturbance history or abundance of large colonies (potential fragment sources) but was negatively correlated with shelf area ($r^2 = 0.57$, $P < 0.01$). We argue that sexual recruitment is more prevalent in the eastern range of *A. palmata* than the west, and that these geographic differences in the contribution of reproductive modes to population structure may be related to habitat characteristics. The two populations of the threatened *A. palmata* differ fundamentally in reproductive character and may respond differently to environmental change.

Key words: Acropora palmata; *asexual reproduction; Caribbean coral; clonality; coral reef; extinction risk; genotypic diversity; microsatellite; phylogeography; recruitment.*

Introduction

Structural species (sensu Connell et al. 1997) build the three-dimensional architecture of ecosystems. Stable population sizes of structural species are therefore beneficial for the demographic persistence and function of entire ecosystems. While this ultimately involves completing the sexual life cycle, many structural species are capable of extensive clonal reproduction, including redwoods (Douhovnikoff et al. 2004), sea grasses (Reusch 2001), and reef corals (Ayre and Hughes 2000). Such clonal growth may allow for population persistence and preservation of genetic diversity through periods of poor sexual recruitment (Lasker and Coffroth 1999). Clonal reproduction may also lead to reduced genotypic diversity and, as a result, higher susceptibility to environmental volatility (Reusch et al. 2005). Knowledge of genetic and genotypic diversity patterns is thus critical for a complete understanding of population structure and function of clonally reproducing structural species.

The consequences of clonal growth for genotypic diversity depend largely on how frequently sexual recruits replenish local populations and how long genets live (Eriksson 1993). Genotypic richness is directly proportional to frequency of sexual recruitment while genotypic evenness is more influenced by genet longevity, a consequence of the size dependency of genet survival (Coffroth and Lasker 1998*b*). Both empirical (Ayre 1985, Hartnett and Bazzaz 1985, Hunter 1993, Travis and Hester 2005) and theoretical studies (Sebens and Thorne 1985) have suggested that genotypic diversity at a local scale might decrease over time

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through elimination of genets by intraspecific competition or stochastic effects. In contrast, genotypic diversity might remain high if sexual recruits, however rare, have a long life span after successful establishment (Burnett et al. 1995, McFadden 1997) and have similar competitive abilities (Ferrell 2005). As a consequence of the complex interplay between the frequency of sexual recruitment, genet longevity, and stochastic effects, the ratio of clonal to sexual recruitment is expected to vary over the geographic range of a species.

For sessile organisms with external fertilization, asexual reproduction may be the only local means of proliferation if population densities decline to a point that dilution of gametes is too great for fertilization to occur (Allee effect; Pennington 1985, Knowlton 1992, Levitan 1992). Such remnant populations may become sexually extinct after prolonged clonal growth and the absence of immigration from other populations (ecologically driven sexual extinction; Honnay and Bossuyt 2005). Sexual extinction becomes more likely in fragmented populations and in populations at the extremes of the species' range due to decreases in the frequency of immigration (Ellstrand and Roose 1987, Eckert 2002, Honnay and Bossuyt 2005). Persistence of clonally reproducing structural species is thus a function of both sexual and asexual reproduction.

Populations of structural species with high genotypic diversity may be able to better cope with extreme climatic events (Reusch et al. 2005) and enhance species diversity in their communities (Booth and Grime 2003). Populations with low clonal diversity are more vulnerable to pathogens and parasites (Lively et al. 1990, Schmid 1994, Zhu et al. 2000, Booth and Grime 2003). Pathogens in coral reef ecosystems may be increasing in both frequency and virulence as sea-surface temperature rises (Ben-Haim et al. 2003, Jones et al. 2004, Rosenberg and Falkovitz 2004). The decline of reef-building acroporids in the Caribbean that began in the 1980s was largely the result of a disease outbreak (white band disease; Gladfelter 1982, Aronson and Precht 2001), with bleaching and hurricanes being additional contributing factors (Knowlton et al. 1981, Woodley et al. 1981). Bak (1983) previously suggested that high asexual reproduction rates might have led to low genotypic diversity and, hence, high disease susceptibility in Caribbean acroporids. Differential sensitivity of genets to environmental extremes has also been suggested for several cnidarians (Shick and Lamb 1977, Lasker et al. 1984, Ayre 1985, Glynn 1990, Lasker 1990, Gleason 1993).

In this study, we investigate the clonal structure of a threatened structural species of Caribbean reefs, the elkhorn coral *Acropora palmata* (Plate 1; also see Appendix A). Prior to major population declines in the 1980s, *Acropora palmata* was the primary constructor of reef framework in many locales such as the Florida Keys (Shinn 1963) and a dominant occupier of space on Caribbean reefs (Shinn 1963). The high cover was likely the result of proliferation via branch breakage by physical disturbance (fragmentation; Highsmith 1982) and high growth rates (Shinn 1966, Gilmore and Hall 1976, Tunnicliffe 1981, Highsmith 1982). The relative importance of clonal structure as it relates to population growth is not clear however, because no studies have examined clonal structure in *A. palmata*. Analyses of clonal structure in *A. palmata*'s congener, *A. cervicornis,* suggested single clones sometimes dominated areas of 10 m^2 in Jamaica and St. Croix (Neigel and Avise 1983), although the genetic basis of tissue compatibility assays underlying this study have been questioned (Heyward and Stoddart 1985, Resing and Ayre 1985).

Clonal reproduction in some corals, including *A. palmata*, is initiated by extrinsic factors similar to some terrestrial plant species (aspen; Gom and Rood 1999) rather than by intrinsic processes (stolon formation, production of asexual larvae). Physical disturbance is the most commonly invoked mechanism responsible for fragmentation leading to clonal proliferation in corals (Hunter 1993, McFadden 1997, Coffroth and Lasker 1998*b*) and large-scale disturbances such as hurricanes occur in somewhat predictable spatial patterns, with higher frequency and intensity in the northwest of the Caribbean (Gardner et al. 2005). Furthermore, acroporid populations should have the chance to adapt to regionally varying disturbance regimes. The externally fertilized larvae of *Acropora palmata* disperse for about one to two weeks in the plankton (Szmant 1986), and multi-locus genotyping suggests larval exchange occurs within, but rarely between, eastern and western phylogeographic provinces (split along a northeast–southwest boundary running between the Mona Passage to the Guajira Peninsula, Colombia, with some mixing in Puerto Rico [Baums et al. 2005*b*, Baums et al. 2006]).

We hypothesized that clonal structure would vary over the geographic range of *A. palmata* under the influence of several intrinsic and extrinsic factors affecting sexual and asexual reproductive potential, including the distinct genetic makeup of the western and eastern phylogeographic provinces of *A. palmata*. Because the geographic scale of variation in clonal structure of *A. palmata* was not known, we employed a hierarchical sampling design: clonal structure and population parameters (such as colony size frequency distribution) were assessed within reefs (30–70 m), between reefs (10–100 km), regions (1000 km), and provinces in the Caribbean. The goals of the study were to (1) assess the geographic scale of variation in clonal structure in *A. palmata* using high resolution microsatellite markers and (2) test whether factors previously proposed to cause variation in clonal structure, such as size distribution of populations, disturbance frequency, or habitat characteristics, explain the patterns we observe.

Materials and Methods

Sampling

A total of 751 *Acropora palmata* Lamarck colonies was sampled and genotyped from 32 stands representing

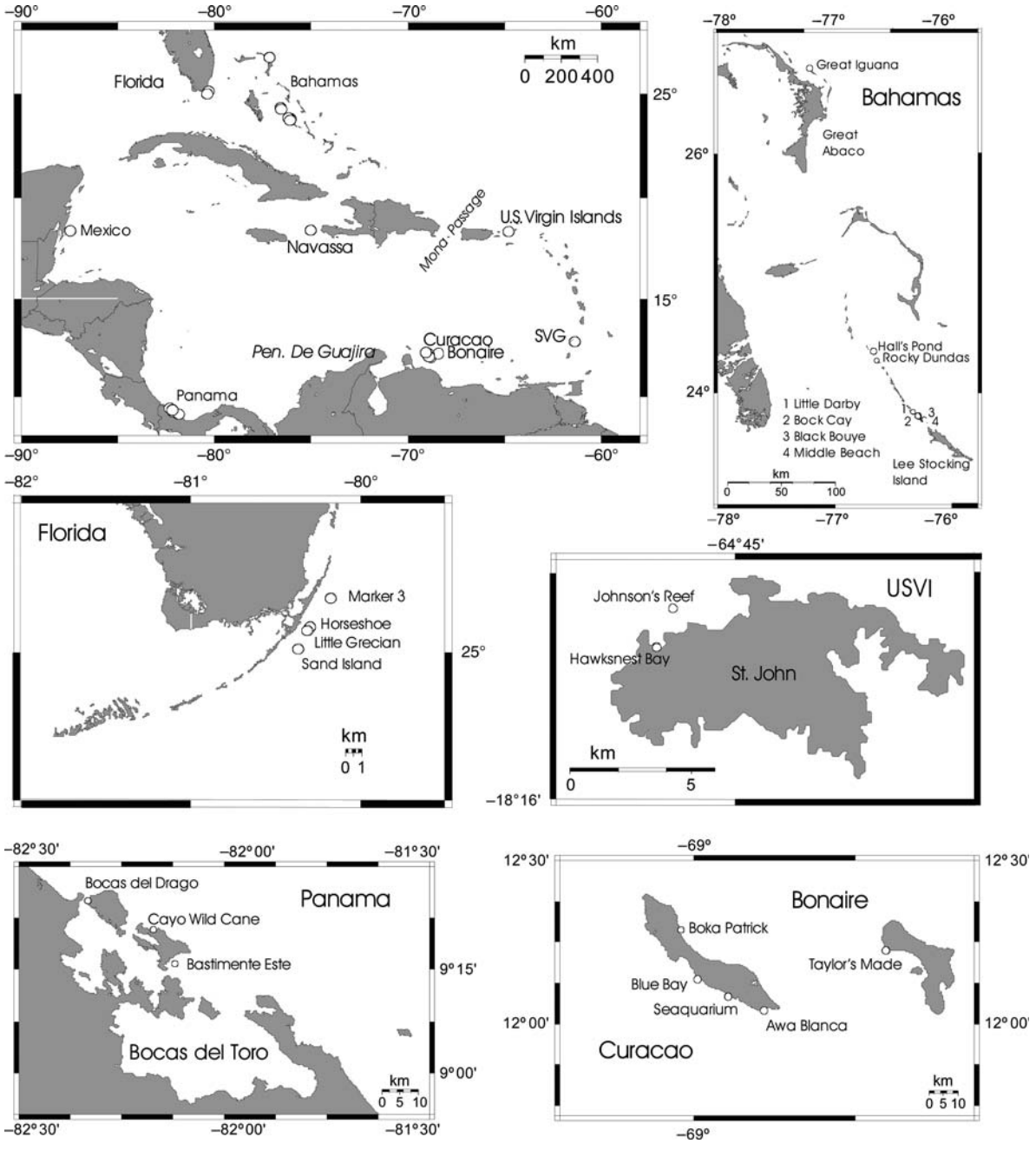

FIG. 1. Geographic localities in the Caribbean from which colonies of *Acropora palmata* were sampled.

26 reefs in eight regions of the Caribbean and western North Atlantic (Fig. 1, Tables 1 and 2; see Table 1 in Baums et al. 2005*b* for GPS coordinates of sampling sites). The eight regions fall into two phylogeographic provinces: populations in Florida, Bahamas, Navassa, Panama, and Mexico belong to the western province; populations in the U.S. Virgin Islands, St. Vincent and the Grenadines, Bonaire, and Curaçao belong to the eastern province (Baums et al. 2005*b*). The term reef is used when referring to duplicate sets of samples (=stands) from the same site. Colonies were sampled on three spatial scales using a random sampling procedure (described in Baums et al. 2005*a*) to detect both common and rare genets. Random numbers were generated by the random number generating function in Microsoft Excel (Microsoft Corporation, Redmond, Washington, USA) as coordinates for locations within each of three nested circles with radii of 15 m, 10 m, and 5 m. These coordinates were generated with a precision of 5° of arc and of 50 cm along strike. Coordinates were

TABLE 1. Characteristics of *Acropora palmata* sampled randomly for analysis of clonal structure.

Region	Reef code	Reef name	Num. col.	Col. dens.	Genet dens.	Prop. sampled	N	N_g	N_g/N	G_o	G_o/G_e	G_o/N_g	$1 - D$	E	Gr
Bahamas	Ba1	Great Iguana	61	0.09	0.010	0.38	23	7	0.30	3.33	0.14	0.48	0.89	0.53	2
	Ba5	Bock Cay	105	0.15	0.011	0.22	23	8	0.35	4.10	0.18	0.51	0.79	0.68	3
	Ba7	Middle Beach	62	0.09	0.014	0.37	23	10	0.43	4.85	0.21	0.49	0.83	0.63	2
Bonaire	Bo1a	Taylors Made I	92	0.13	0.020	0.23	21	14	0.67	10.26	0.49	0.73	0.95	0.75	3
	Bo1b	Taylors Made II	52	0.07	0.025	0.42	22	18	0.82	13.44	0.61	0.75	0.97	0.40	3
Curaçao	Cu1a	Blue Bay I	131	0.19	0.018	0.16	21	13	0.62	4.74	0.23	0.36	0.83	0.00	2
	Cu1b	Blue Bay II	78	0.11	0.027	0.26	20	19	0.95	18.18	0.91	0.96	0.99	0.00	4
	Cu2a	Sea Aquarium I	560	0.79	0.018	0.04	22	13	0.59	8.07	0.37	0.62	0.80	0.41	3
	Cu2b	Sea Aquarium II	370	0.52	0.017	0.07	25	12	0.48	4.06	0.17	0.34	0.90	0.81	2
	Cu3a	Awa Blanca I	160	0.23	0.023	0.13	21	16	0.76	11.92	0.57	0.74	0.96	0.60	3
	Cu3b	Awa Blanca II	200	0.28	0.017	0.11	22	12	0.55	8.64	0.39	0.72	0.93	0.83	3
Florida	Fl4	Horseshoe	175	0.25	0.001	0.11	20	1	0.05	1.00	0.05	1.00	0	0	1
	Fl5	Little Grecian	131	0.19	0.001	0.15	20	1	0.05	1.00	0.05	1.00	0	0	1
Panama	Pa1	Bocas Del Drago	156	0.22	0.013	0.14	22	9	0.41	3.06	0.14	0.34	0.71	0.31	2
	Pa3a	Bastimentos I	102	0.14	0.007	0.21	21	5	0.24	1.68	0.08	0.34	0.42	0.15	2
	Pa3b	Bastimentos II	107	0.15	0.018	0.19	20	13	0.65	10.00	0.50	0.77	0.95	0.80	3
USVI	Vi1	Johnson's Reef	204	0.29	0.023	0.11	23	16	0.70	11.76	0.51	0.73	0.96	0.74	3
	Vi2a	Hawksnest Bay I	264	0.37	0.011	0.08	22	8	0.36	3.32	0.15	0.41	0.73	0.50	2
	Vi2b	Hawksnest Bay II	212	0.30	0.013	0.11	24	9	0.38	3.06	0.13	0.34	0.70	0.38	2
Navassa	Na3	Lulu Bay	NA				15	15	1.00	15	1	1	1.00	ND	4
Total		14 reefs (20 populations)	3222				430	219							
Mean			169.6	0.24	0.02	0.18	21.5	11.0	0.52	7.07	0.34	0.63	0.77	0.45	
SD			123.1	0.17	0.01	0.11	2.1	5.0	0.26	5.06	0.28	0.24	0.30	0.30	

Notes: Duplicate sets of circles were collected at some reefs (indicated by the "a" or "b" ending of the reef code). Total area sampled was always 707 m^2. Key to abbreviations: Num. col., number of colonies within each set of circles; N, number of colonies that were sampled; Prop. sampled, proportion of colonies of those present that were sampled; Col. dens., colony density (no./m^2); Genet dens., genet density (no./m^2); N_g, number of genets; G_o, observed genotypic diversity; G_e, expected genotypic diversity; G_o/G_e, genotypic diversity (assesses the relative importance of sexual reproduction in a population); G_o/N_g, genotypic evenness (number of ramets per genet); $1 - D$, complement of Simpson's diversity index; E, Fager's evenness; NA, data not available; ND, not defined. Populations were classified into groups (Gr) based on their combination of N_g/N and G_o/G_e values as asexual (1), mostly asexual (2), mostly sexual (3), and sexual (4) (Fig. 3).

located using a compass and a measuring tape attached to a stake placed in the center of the stand. The colony underneath each coordinate was sampled until eight samples per circle were obtained. If there was no colony at a particular random coordinate, that coordinate was crossed out and the next random number was sampled. No colony was sampled twice. By design, this approach results in higher sampling effort on the 5-m scale compared to the 10- and 15-m scales. All colonies within the 15 m radius circle were counted so that colony density (no. colonies/m^2) at each site could be estimated. A colony (ramet) is defined as a continuous, upright entity of skeleton with a stalk that attaches it to the bottom. Where the size of the *Acropora palmata* stand

TABLE 2. Characteristics of *A. palmata* stands sampled haphazardly for analysis of clonal structure.

Region	Reef code	Reef name	Colonies present	Max. dist. sampled (m)	Prop. sampled	N	N_g	N_g/N	G_o	G_o/G_e	G_o/N_g	$1 - D$	E	Gr
Bahamas	Ba6	Black Buoy	NA	14.4	NA	21	11	0.52	7.23	0.34	0.66	0.90	0.77	3
	Ba2	Halls Pond	23	67.3	0.83	19	12	0.63	9.76	0.51	0.81	0.95	0.85	3
	Ba4	Little Darby	NA	21.6	NA	25	10	0.40	3.81	0.15	0.38	0.77	0.49	2
	Ba3	Rocky Dundas	NA	55.2	NA	17	4	0.24	2.43	0.14	0.61	0.63	0.63	2
Curaçao	Cu4	Boka Patrick	NA	72.0	NA	21	15	0.71	12.60	0.60	0.84	0.97	0.83	3
Florida	Fl9	Marker 3	NA	49.0	NA	40	2	0.05	1.05	0.03	0.53	0.05	0.00	2
	Fl3	Sand Island	75	87.1	0.75	39	12	0.21	3.25	0.06	0.27	0.71	0.60	3
Mexico	Me1	Chinchorro	NA	60.0	NA	56	7	0.20	2.58	0.07	0.37	0.63	0.55	2
Navassa	Na1	N Shelf	19	44.1	0.95	35	18	1.00	18.00	1.00	1.00	1.00	ND	4
	Na2	NW Point	37	96.2	0.95	18	35	1.00	35.00	1.00	1.00	1.00	ND	4
Panama	Pa2	Cayo Wild Cayne	21	34.2	0.81	35	7	0.41	3.11	0.18	0.44	0.72	0.40	4
SVG	Sv4	Canouan	NA	86.3	NA	17	12	0.71	8.26	0.49	0.69	0.97	0.79	3
Total		12 reefs				321	145							
Mean				78.9		26.8	12.08	0.51	8.92	0.38	0.64	0.77	0.59	
SD				89.4		12.3	8.49	0.31	9.61	0.35	0.25	0.27	0.26	

Notes: When available, the total number of colonies present is given. Max. dist. sampled is the maximum distance between samples (not genets) collected and indicates the sampling scale. See Table 1 legend for explanation of other abbreviations. Colony densities were 0.012 and 0.005 colonies/m^2 for N Shelf and NW Point Reef, respectively.

PLATE 1. Colony morphology of Caribbean elkhorn coral (*Acropora palmata*) varies from plating to branching to encrusting. Shown is an example of branching morphology from Blue Bay II, Curacao, 155 × 120 × 105 cm. A color version of Plate 1 is provided in Appendix A. Photo credit: I. Baums.

allowed, two nonoverlapping, duplicate sets of circles were sampled (noted by the lowercase letters a and b as part of the reef code in Table 1). Distances between center points of duplicate sets of circles ranged from 35 m to 70 m.

This random approach was not always feasible, especially when colony density was low. In these cases, either all or a large proportion of the colonies present at a site were sampled haphazardly (Table 2). When feasible, the total number of colonies present at the site was counted (Table 2). The sampling scale for haphazardly sampled sites was estimated by calculating the maximum pair-wise distance between samples. In the following discussion, we define a population as all samples originating from one set of nested circles or from one haphazardly sampled reef. For randomly and haphazardly sampled sites, maps were prepared identifying the location of each colony in relation to the center point. Colony size was measured as two diameters and the height to the nearest 10 cm. Active disease occurrence ("white diseases," apparent as a sharp front between live tissue and bright white dead skeleton) and the number of coral-eating snails (*Coralliophila abbreviata*) were recorded at time of sampling at most sites. One 1 cm long tip was snipped off from each identified colony using a bolt cutter and placed in a labeled zip bag. Coral samples were transferred into 70% ethanol upon returning to shore and stored at −80°C until genotyping.

Genotyping

We refer to an assemblage of genetically identical colonies (clones) that are descendants of a single zygote as a "genet" (Harper 1977, Hughes 1989, Carvalho 1994). Physiologically distinct colonies that can function and survive on their own but belong to the same genet are termed "ramets" (Kays and Harper 1974) or clone mates.

We used five newly developed microsatellite loci for *Acropora palmata* (Baums et al. 2005*a*) to distinguish genets. Because these markers are highly heterozygous (mean observed heterozygosity = 0.88), there is a low probability of identifying two colonies as clone mates when in fact they are distinct genets (this is called the probability of identity (PI) and equals 1×10^{-7}) (Baums et al. 2005*b*). Microsatellites were shown to be Mendelian and coral specific by controlled crosses (Baums et al. 2005*a*).

Tissue samples were extracted and genotyped as described in (Baums et al. 2005*a*). Briefly, two multiplex polymerase chain reactions (PCR) were performed per sample using fluorescently labeled primers to assay five microsatellite loci containing AAT repeats. PCR products were visualized with an automated sequencer (ABI 3730; Applied Biosystems, Foster City, California,

USA). An internal size standard (Gene Scan 500-Liz; Applied Biosystems) ensured accurate sizing. Electropherograms were analyzed with GeneMapper Software 3.0 (Applied Biosystems). Alleles were scored based on amplicon size. Samples with identical alleles at all five loci were regarded as ramets belonging to the same genet.

Analyses

Genotypic vs. genetic diversity.—Genotypic and genetic diversity describe fundamentally different processes that are at the heart of this study. Genetic diversity refers to the amount of variation on the level of individual genes in a population. In contrast, genotypic diversity is defined as the number of unique multilocus genotypes present in a population and varies on the level of whole organisms. A multilocus genotype (genet) may occur several times (ramets) in a population only as a result of asexual replication (identity by descent).

1. *Adequacy of sampling approach.*—Unless one genet completely dominates a population, the number of genets detected increases with sample size, sampling intensity (i.e., proportion of the population sampled), and the spatial scale of sampling. To standardize data sets from different populations sampled at different intensities and spatial scales (Tables 1 and 2), rarefaction curves were calculated (Gotelli and Colwell 2001). By repeatedly resampling the pool of N colonies, the average number of genets represented by 1 to N individuals is obtained and plotted. Biases are likely to differ between randomly and haphazardly sampled reefs (see *Materials and Methods: Sampling*) and so only samples collected using similar protocols can be compared in this manner (Gotelli and Colwell 2001). Rarefaction analysis was carried out using Analytic Rarefaction, version 1.3, based on the formulation of Tipper (1979; software *available online*).[5]

2. *Clonal structure parameters.*—Clonal population structure was expressed as genotypic richness (standardized to sample size N_g/N), genotypic diversity (G_o/G_e), or genotypic evenness (G_o/N_g; sensu Coffroth and Lasker 1998*b*). Genotypic richness is given as the number of unique genotypes (genets, N_g) identified over the total number of colonies sampled (N). Observed genotypic diversity, G_o, as defined by Stoddart and Taylor (1988) was calculated as

$$G_o = \frac{1}{\sum_i^k g_i^2}$$

where g_i is the relative frequency of the ith of k genotypes. An expected level of genotypic diversity equal to N can be posed for a sexually reproducing population. The multilocus genotypes produced by the five microsatellite markers in this study were unique to each genet (see *Materials and Methods: Genotyping*), so that the genotypic diversity expected in solely sexually reproducing population (G_e) equals the number of colonies genotyped (n). Previous studies using less polymorphic allozyme markers had to estimate G_e (Stoddart and Taylor 1988). The ratio G_o/G_e attempts to measure the relative contribution of asexual and sexual reproduction in a population and is a measure of the populations' genotypic diversity. G_o/G_e has a maximum of 1 in a solely sexual population and approaches 0 in a population dominated by a single genet.

The ratio G_o/N_g measures genotypic evenness. In a population with one or a few dominant clones, the evenness approaches 0, whereas, in a population where each genet is represented by equal numbers of ramets, the ratio approaches 1. A peculiarity of this statistic is that populations with only one genotype also have an evenness of 1 although, arguably, evenness has no meaning in a population with a single genet. A wide range of combinations of genotypic diversity and evenness values are possible in a given population and are in fact observed in clonal plants (e.g., Sole et al. 2004). Thus, based on the combination of genotypic diversity (G_o/G_e) and evenness (G_o/N_g), populations were classified into four groups (sexual, mostly sexual, asexual, and mostly asexual) to facilitate discussion and further analysis.

For comparison with the plant literature (Ellstrand and Roose 1987), two additional measures of dominance and evenness are presented. The complement of the Simpson index corrected for finite samples, D (Pielou 1969), was calculated as

$$D = 1 - \left[\frac{\sum n_i(n_i - 1)}{N(N-1)}\right]$$

where n_i is the number of colonies of genotype i and N is the total sample size. D is 0 in a population with only one genet and 1 in a population comprised of genets with only one member. The evenness measure of Fager (1972), was calculated as

$$E = \frac{D_{obs} - D_{min}}{D_{max} - D_{min}}$$

where $D_{min} = (N_g - 1)(2N - N_g)/N(N-1)$ and $D_{max} = N(N_g - 1)/N_g(N-1)$. E is 0 in a population where all colonies represent different genets or where all colonies belong to the same genet. E is undefined when all genets of a population have the same number of ramets.

3. *Ecological parameters and their relationship to clonal structure among populations.*—Several ecological characteristics of the sampled populations were recorded at the time the tissue samples were collected. Colony density was expressed as the number of colonies counted within the sample area (see *Materials and Methods: Sampling*). Data on colony density was available for 19 populations (Table 1). Size histograms for the sampled

[5] ⟨http://www.uga.edu/strata/software/Software.html⟩

colonies based on estimated colony volume (product of two orthogonal diameters and one height) were prepared for each population (data not shown). The distribution of size classes was skewed toward small colonies. Hence, size estimates were log transformed and then mean size of colonies was compared among groups (via ANOVA described in *Materials and Methods: Analyses: Potential factors influencing clonal structure*). In addition, the coefficient of variation (CV) of log-transformed size estimates for each reef was calculated. The CV provided estimates of the skewness of size frequency distributions in the different populations.

The spread of ramets was expressed as the average distance between clone mates (m). First, radial sampling coordinates were converted to X–Y distances. Then, pairwise comparisons of distance (in m) were made between all ramets of a genet and averaged. Note that this average can be based on very different numbers of n (Fig. 2). The maximum extent of genets on a reef was measured as the maximum distance (in m) between any two ramets of a genet in that population.

We used one-way ANOVAs followed by Tukey's post hoc tests to examine significant differences between populations of different clonal structure groups (asexual, mostly asexual, mostly sexual and sexual, see above) in colony density, size structure, and clonal spread. Variances were homogenous for all comparisons (Levene's test, $P > 0.05$).

To assess the spatial scale at which clonal structure varies predictably, population values of genetic and ecological parameters were averaged by sampling region ($n = 8$) and by province ($n = 2$ with four regions each). Regression analysis was performed to test for significant correlation between ecological parameters and clonal structure within each province. We tested for significant differences in clonal structure and ecological parameters between provinces using an independent t test after homogeneity of variances was ascertained (Levene's test).

4. *Potential factors influencing clonal structure*.—In previous studies (Hunter 1993, Lirman 2000*a*), physical disturbance, habitat availability, and size structure of the population were identified as important factors in determining the degree of clonality in local populations of scleractinian corals. Existing data sets (for physical disturbance and habitat availability) and the ecological data collected in the present sampling (for size structure) were used to estimate these parameters for each of the randomly sampled populations. A stepwise regression assessed the capacity of these independent factors to explain spatial patterns in clonal structure.

We quantified the number of hurricanes experienced by each of the randomly surveyed sampling sites between 1863 and 2003 (Table 1) using GIS (geographical information system, ArcView version 3.2; ESRI, Redlands, California, USA). Standard buffer zones around each reef location were defined (Stoddart et al. 1985, Done 1992, Gardner et al. 2005) according to storm strength: 35-km buffer for tropical storms (TS) and category 1 and 2 hurricanes (HS 1 and HS 2); 60 km buffer for category 3 hurricanes (HS 3); 100 km buffer for category 4 and 5 hurricanes (HS 4 and HS 5). Spatially explicit data on hurricane occurrence and strength for the Caribbean basin are *available online*.[6] Using this data set, each storm was counted once when it entered its strength-specific buffer zone.

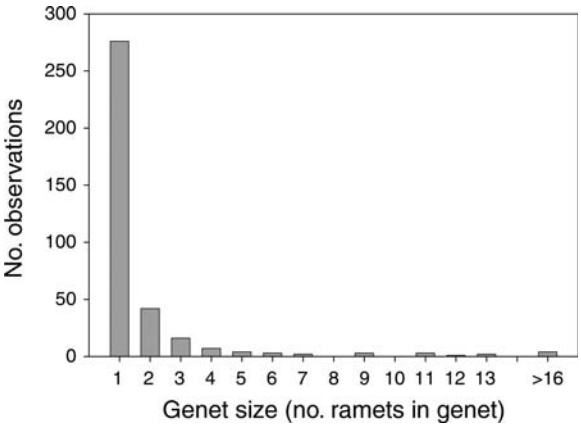

FIG. 2. Frequency of genet size (no. sampled ramets in a genet) in Caribbean *A. palmata*. In total, $n = 364$ genets were observed, containing a total of $n = 751$ ramets.

Caribbean reefs occur on and around land masses of diverse geological origin such as continental shelves (e.g., reefs off Florida and Panama), volcanic islands (e.g., St. Vincent and the Grenadines), and banks (e.g., the Bahamas). These habitats are characterized by differences in reef slope and thus total habitat area available above 30 m. Habitat area was measured by calculating the amount of area contained in each of 30 1-m depth increments from 0 to −30 m using bathymetry with 1-km resolution in a 35 km area around the randomly sampled reefs (using Arc View 3.2; bathymetry data *available online*).[7] This measure gives an indication of how steep the slope is surrounding the sampled locations.

Fragmentation processes are related to colony size in *Acropora palmata* (Lirman 2000*a*). Large colonies are likely the greatest source of fragments (asexual reproduction) because they have large numbers of branches (potential fragments) and their size enhances chances of successful recovery from injuries associated with fragmentation (Lirman 2000*b*). Colony volumes were log-transformed and binned. The number of large colonies in each randomly sampled population was determined by counting the number of colonies that had a log transformed volume index ≥ 6. This represents the upper third of the log size classes observed among the reefs (bins ranged from 2 to 8 in 0.5 increments).

[6] ⟨http://hurricane.csc.noaa.gov/hurricanes/⟩
[7] ⟨www.reefsatrisk.com⟩

Measures of habitat availability, physical disturbance, and abundance of large colonies were entered into a multiple linear regression analysis with N_g/N (genotypic richness) as the dependent variable (SPSS version 9.0; SPSS, Inc., Chicago, Illinois, USA). We confirmed with correlation analysis that the three independent factors were not correlated. The model was run twice, once with backward and once with forward addition of factors. Similar regression coefficients were obtained in both cases.

Results

Among the 751 *Acropora palmata* colonies sampled from throughout the Caribbean, there were 364 unique genotypes. Most genets were represented by a single ramet (Fig. 2). One genet from Horseshoe Reef, Florida, however, was composed of 20 sampled ramets over an area of 707 m^2 (Table 1).

Adequacy of sampling approach

Rarefaction curves (not shown) were compared for the set of randomly sampled populations, and for the set of haphazardly sampled populations. The number of genets present clearly differed between populations, even when comparing them at the level of the smallest sample size ($n = 17$ from Rocky Dundas for haphazardly sampled reefs and $n = 15$ from Lulu Bay for randomly sampled reefs; Tables 1 and 2). The ranking of populations in terms of the number of genets present remained the same at these reduced sample sizes as for at their full sample size. Thus, in the following, raw non-standardized data are used to describe clonal structure patterns to prevent the loss of information associated with rarefaction curves (Gotelli and Colwell 2001).

Second, to test whether genotyping 24 samples on a 15-m (or smaller) scale is adequate for estimating the total number of genotypes at a site, we compared the number of genets identified in the nested, randomly sampled circles. Most of the clonal richness of a population was captured by the eight samples collected on the smallest (5 m) radius plot (mean ± SD of 3.8 ± 2 genets detected, $n = 73$). Widening the radius from 5 m to 10 m (4.9 ± 2, $n = 93$) and then again to 15 m (5.1 ± 2, $n = 97$) resulted in small, nonsignificant gains in the number of genets identified (one-way ANOVA, $P > 0.1$).

Variation in population structure within and among reefs

Clonal population structure.—Genotypic richness (N_g/N) ranged from 1 (each sample representing a unique genotype) on all three Navassa reefs (Fig. 3A) to nearly 0 (only one genet present) on two Florida reefs (Fig 3B; also see the Supplement). The Caribbean-wide average of N_g/N was 0.51 ± 0.28. At the 14 reefs randomly sampled using the nested circle approach, genotypic richness averaged 0.52 ± 0.26. This value was virtually identical to that for haphazardly sampled reefs (0.51 ± 0.31), despite the potential bias toward detecting a larger number of genets when sampling a larger proportion of the population with the haphazard sampling approach.

Genotypic diversity, richness, and evenness of sampled *A. palmata* populations show a continuum between 0 and 1 for all measures (Tables 1 and 2). Inspection of the relationship between genotypic diversity and evenness values distinguishes four groupings of population structures (Fig. 4, Tables 1 and 2). Four populations (all three Navassa reefs and one population from Blue Bay, Curaçao) were classified as sexual with an average genotypic diversity of 0.98 ± 0.05, indicating that asexual reproduction is nearly absent. This results in high genotypic evenness values (1.00 ± 0.03). The "mostly sexual" group was characterized by moderate genotypic diversity (0.44 ± 0.14) and evenness (0.69 ± 0.11) values. While some asexual reproduction occurs, no one genet dominates these populations. This group consisted of 12 populations. "Mostly asexual" populations ($n = 13$) had low genotypic diversity (0.13 ± 0.06) and evenness (0.40 ± 0.09). Here, one or a few clones dominated the population. In two populations, Horseshoe and Little Grecian reefs in Florida, only one genet was identified (see Figs. 3 and 4 in Baums et al. 2005*a*). Both stands are linear in shape (I. B. Baums, *personal observation*) and additional samples ($n = 4$ and 5, respectively, Fig. 3B) collected from the edges of the stands (27.5 ± 11.8 m and 58.2 ± 8.4 m distance to center point, respectively) confirmed that each was monoclonal. At Little Grecian reef, the maximum extent of the genet we sampled was 75.3 m. At Horseshoe reef, the maximum distance we sampled was 69.7 m. The relationship between G_o/N_g and G_o/G_e is a power function ($f = 0.99x^{0.42}$, $r^2 = 0.86$, $P < 0.001$, excluding the asexual group, see *Materials and Methods*). The addition of just one genet to a mostly asexual population results in a relatively higher gain in evenness than the addition of one genet to a mostly sexual population. Similar patterns of clonal diversity and evenness were evident when using Simpson's diversity index ($1 - D$) and Fager's evenness measure (E, Tables 1 and 2) to obtain the groupings in Fig. 4.

In three cases, duplicate sets of circles sampled on the same reef within 50–75 m of one another resulted in such different estimates of clonal diversity and evenness that duplicates were placed in different population structure groups (Table 1, Fig. 4). One duplicate set from Sea Aquarium, Curaçao, was placed into the mostly asexual group, whereas the other was placed into the mostly sexual group. The same was true for the duplicate sets from Bastimentos, Panama. Duplicate sets from Blue Bay, Curaçao, showed such different patterns of clonal structure as to warrant classification for one as mostly asexual whereas the other was sexual (Table 1, Fig. 4).

At the scale of reefs, similar variation was observed. In the Florida Keys, Horseshoe and Little Grecian Reefs are separated from Sand Island by only 15 km, and have similar depth and exposure but contrasting clonal structure. Johnson's Reef and Hawksnest Bay Reef in

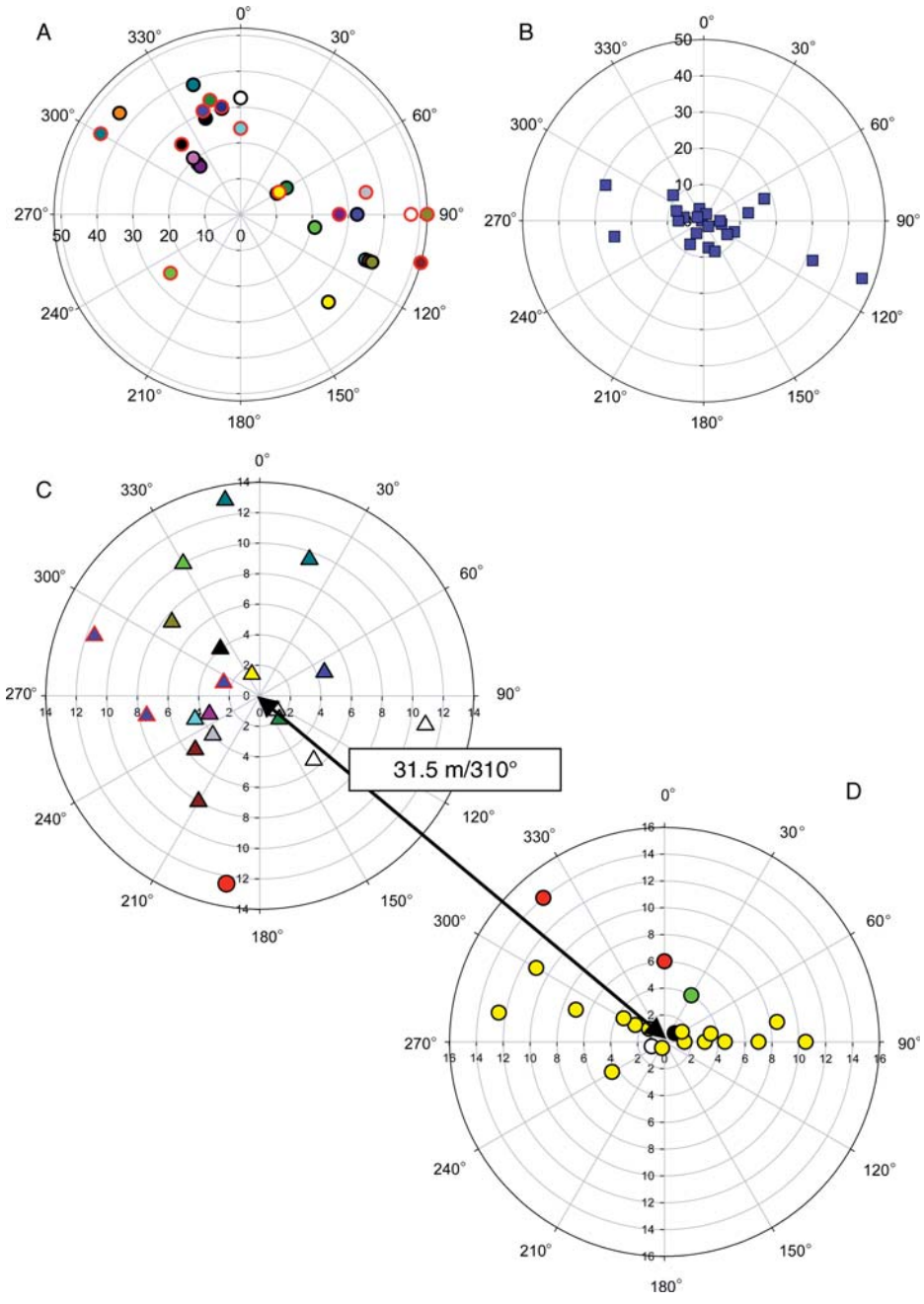

FIG. 3. Representative polar plot maps of genotypic diversity within populations of *A. palmata*. Each colored symbol represents a sampled ramet. Ramets of the same genet are indicated by a common symbol and color. The radial axis shows the distance (m); the angular axis shows the angle in degrees. (A) At NW Point reef, Navassa, every colony represents a unique genet. (B) At Horseshoe Reef, Florida, each point represents a ramet of the same genet. At Bastimentos Reef in Panama, clonal structure varies between (C) stand I and (D) stand II, even though these are only 31.5 m apart (distance between center points at 310°). One genet (red with black outline) occurred at both reefs. The plots are arranged graphically as they were laid out on the reef. See Tables 1 and 2 for sample sizes.

the USVI, separated by just 2 km, also had markedly different degrees of asexual reproduction (Table 1).

Ecological parameters and their relationship to clonal structure.—Colony density varied considerably among the sampled stands, from 0.09 to 0.79 colonies/m^2, however, there was no significant difference in colony density among the populations in the four clonal structure groups (one-way ANOVA, $F_{3,15} = 1.20$, $P = 0.34$). Similarly, neither mean colony size nor the variation in size structure (data not shown) differed

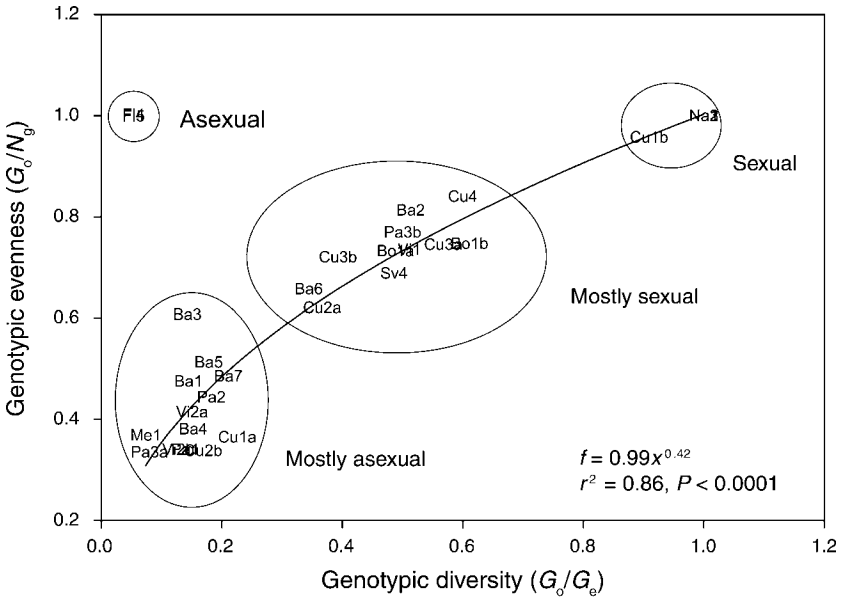

FIG. 4. Clonal structure of *A. palmata* stands ($n = 32$) in the Caribbean. Based on the combination of genotypic evenness (G_o/N_g) and genotypic diversity (G_o/G_e), stands are divided into four groups ranging from asexual to sexual to facilitate further analysis. The power function shown was fitted excluding the asexual Florida populations (Fl4 and Fl5) because the statistic G_o/N_g approaches zero with low evenness, but becomes 1 when G_o equals N_g. Some of the population names are overlapping because these populations share the same combination of G_o/N_g and G_o/G_e (e.g., the two monotypic populations from Florida, F14 and F15).

significantly among the different clonal structure groups (one-way ANOVAs, $F_{3,27} = 0.812$, $P = 0.499$ and $F_{3,27} = 2.33$, $P = 0.096$). The sexual group did have less variation in size structure than the mostly sexual group, probably due to the smaller n.

As is apparent from radial plots (Fig. 3 and Appendix B), clone mates tend to be clumped. Nevertheless, some ramet-rich clones were spread over large areas. Because estimates of clonal spread are sensitive to the area sampled, only stands sampled over similar areas (Table 1) are considered here. Note also that the spatial scale of our sampling appears to be smaller than that of some of the largest clones (e.g., at the monoclonal sites), so our estimates of clonal spread should be biased downward. Populations dominated by one or a few clones (the mostly asexual group) showed significantly larger average clonal spread than populations with fewer ramets per genet (the mostly sexual group; one-way ANOVA, $F_{3,28} = 10.40$, $P < 0.001$). Average clonal spread ($\pm$SD) for each of the four groups was 6.8 $\pm$ 2.2 m (asexual), 4.7 $\pm$ 1.6 m (mostly asexual), 3.2 $\pm$ 1.8 m (mostly sexual), and 2.8 $\pm$ 4.8 m (sexual, not zero due to one genet with two ramets in the Blue Bay II population). Maximum distance between ramets decreased with increasing sexuality (data not shown).

Disease prevalence was at such low levels that a further statistical analysis was not feasible. Out of 545 colonies surveyed, 35 showed signs of disease (Taylors Made $n = 4$, Blue Bay $n = 5$, Sea Aquarium $n = 6$, Awa Blanca $n = 4$, Sand Island $n = 7$, Little Grecian $n = 1$, Horseshoe $n = 3$, Chinchorro $n = 3$, Lulu Bay $n = 1$).

Variation in clonal structure within and among regions and provinces

Within the western province (populations in Florida, Bahamas, Navassa, Panama, and Mexico), both purely sexual ($n = 3$ in Navassa) and purely asexual ($n = 2$ in Florida) populations were observed (Tables 1 and 2). Overall, genotypic richness (N_g/N) was 0.43 $\pm$ 0.31 in this province (Table 3). The large variation of this estimate is due to the entirely sexual populations in Navassa. When excluding Navassa (because it is the only region with entirely sexual populations, which may be due to its exceptionally small shelf area; see *Discussion*, Fig. 6B), mean N_g/N for the western province equaled 0.32 $\pm$ 0.19 (Table 3). Genotypic richness was greater and more homogeneous (mean $N_g/N = 0.64 \pm 0.17$) in the eastern (U.S. Virgin Islands, St. Vincent and the Grenadines, Bonaire, and Curaçao; Table 3) than the western province. Excluding Navassa, the western populations also have lower genotypic diversity than populations in the eastern Caribbean ($G_o/G_e = 0.18 \pm 0.15$ vs. 0.43 $\pm$ 0.23, $P < 0.001$; Table 3). This pattern holds when using the complement of Simpson's diversity index instead of G_o/G_e ($P < 0.01$, Table 3). *Acropora palmata* populations within the sampled areas in the western Caribbean are also less dense (0.13 $\pm$ 0.08 vs. 0.30 $\pm$ 0.21 colonies/m^2, $P < 0.05$, including Navassa) than in the eastern Caribbean (Table 3). Genotypic evenness, spread of clones, and colony size were similar in both provinces (Table 3).

Within each province, genotypic richness (N_g/N; east, $r^2 = 0.55$; west, $r^2 = 0.65$; $P < 0.001$) and genotypic

TABLE 3. Clonal structure of *A. palmata* in each province. Values are means with SD in parentheses.

Province	Col. dens.	N_g/N	G_o/G_e	G_o/N_g	$1 - D$	E	Colony size	Genet spread
West	0.13* (0.08)	0.43* (0.31)	0.31 (0.34)	0.63 (0.27)	0.68* (0.33)	0.50‡ (0.26)	5.16 (0.74)	7.10 (5.12)
West without Navassa	0.17† (0.06)	0.32*** (0.19)	0.18*** (0.15)	0.57 (0.23)	0.60** (0.33)	0.50‡ (0.26)	4.98 (0.76)	8.11 (4.58)
East	0.3 (0.21)	0.64 (0.17)	0.43 (0.23)	0.63 (0.2)	0.9 (0.1)	0.54 (0.29)	5.17 (0.54)	6.65 (2.94)

Notes: See legend of Table 1 for abbreviations. Colony size is expressed as the mean of log(length × width × height). Genet spread is the mean distance (m) between clone mates, and was calculated based on randomly sampled stands only (Table 1). West without Navassa values are for the western province excluding Navassa (see *Results: Variation in clonal structures within and among regions and provinces* for explanation). Clonal structure statistics were tested for significant differences between the eastern and western provinces (with and without Navassa) with *t* tests.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; † $P = 0.056$.

‡ Because E is not defined for populations with only one genet (all Navassa stands), averages of E for the western province with and without Navassa are identical.

diversity (G_o/G_e; east, $r^2 = 0.49$; west, $r^2 = 0.66$; $P < 0.001$) were negatively related to colony density (Fig. 5), indicating that within provinces, denser populations maybe the result of asexual recruitment and that they have lower diversity than less dense populations. Within provinces, clonal spread and mean colony size did not vary with genotypic richness (N_g/N) or genotypic diversity (G_o/G_e) (data not shown).

Factors influencing clonal structure

Multiple linear regressions with the factors shelf area, hurricane incidence, and abundance of large colonies (Fig. 6) against N_g/N explained a maximum of 69% of the variation in genotypic richness and were significant ($P < 0.01$, Table 4). Shelf area explained the most variation (57%), while abundance of large colonies and hurricane incidence were not significant (Table 4, coefficients). However, shelf area does not differ in a predictable manner between the east and the west (Fig. 6A–C).

DISCUSSION

Clonal structure in *Acropora palmata* varied widely among populations, from nearly monoclonal populations in Florida to highly genotypically diverse populations (e.g., Blue Bay II in Curaçao) where each ramet was genetically unique. Reusch et al (2000) found similar extremes in clonal structure among populations of the sea grass *Zostera marina*, but their most genotypically depauperate populations were restricted to geographical extremes (the eastern Pacific and the Baltic) of that species' range. The pattern we found in *A. palmata* was predictable at large geographical scales that coincided with previously identified genetically isolated provinces in the Caribbean. The western province was characterized by genotypically depauperate populations with low colony densities (with one exception), while dense genotypically diverse stands typified the east. We think that variable success of sexual recruitment is driving the observed differences in clonal structure. However, local variation in rates of fragmentation, history of hurricane damage, and size structure of the population may be additional factors influencing the degree of asexuality within provinces, regions, and reefs.

Patterns of clonal structure in Acropora palmata

The scale at which the contribution of asexual reproduction varied can be quite small. *A. palmata* stands separated by only tens of meters within reefs to a few kilometers between reefs showed markedly different patterns in asexual reproduction (Table 1, Fig. 3C, D). Neither colony size, variation in colony size, nor spread

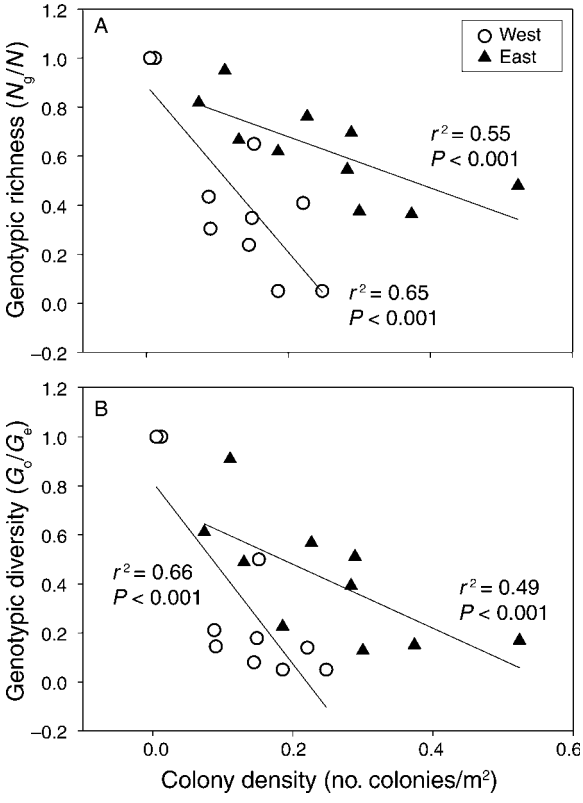

FIG. 5. Relationship between colony density and (A) degree of sexual reproduction (N_g/N) and (B) genotypic diversity (G_o/G_e) in *A. palmata* populations from the two phylogeographic provinces (east and west) of the Caribbean. Higher colony density is associated with (A) a lower degree of sexual reproduction and (B) a lower genotypic diversity within each of the two provinces. *P* values are for linear least-squares regression; $n = 10$ populations in each province.

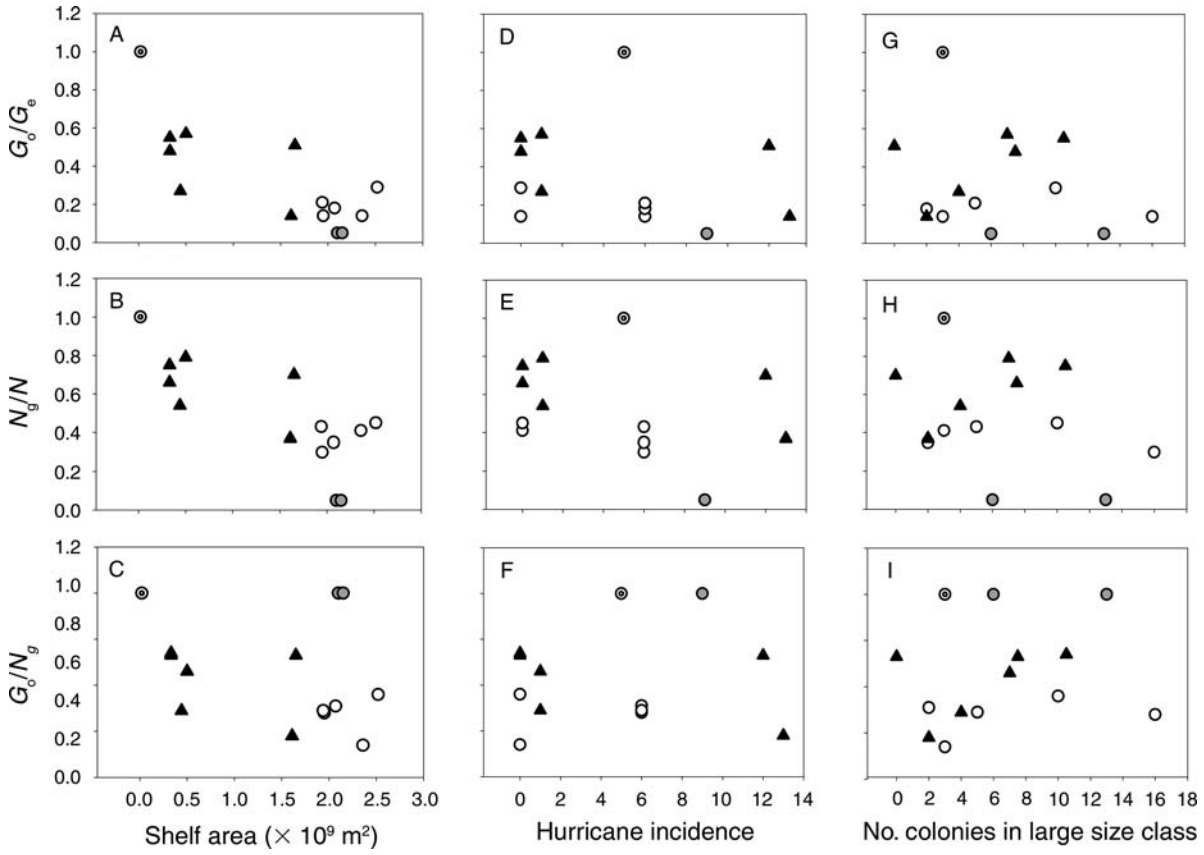

FIG. 6. Relationship between clonal structure of *A. palmata* population and factors potentially influencing clonal structure. Potential factors include (A–C) shelf area above 30 m, (D–F) hurricane incidence, and (G–I) the number of colonies in large size classes that may act as fragment sources. Clonal structure parameters were clonal diversity, G_o/G_e (A, D, G); richness, N_g/N (B, E, H); and evenness, G_o/N_g (C, F, I). When two stands were sampled per reef (stands designated as a or b in Table 1), values describing the clonal population structure were averaged. Circles represent stands from the western province; triangles represent stands from the eastern province. Stands with extremely high (Navassa, circle with center dot) and extremely low (Florida, circles with gray fill) clonal diversity are indicated. Hurricane incidence is the number of hurricanes normalized by storm strength.

TABLE 4. Stepwise linear regressions between N_g/N (the contribution of asexual reproduction to the reef) and several explanatory variables: shelf area above 30 m, hurricane incidence, and abundance of large colonies in each population (see *Materials and Methods: Analyses: Potential factors influencing clonal structure* for an explanation of how these were estimated).

A) Regression analysis

Model	df	F	P	r	r^2	Adjusted r^2	SE
1	3, 10	7.52	<0.01	0.83	0.69	0.60	0.17
2	2, 11	10.22	<0.01	0.81	0.65	0.59	0.17
3	1, 12	15.91	<0.01	0.76	0.57	0.53	0.18

B) Coefficient analysis

Model	Predictors	Standardized coefficient (β)	t	P
1	constant		8.47	<0.001
	shelf area	−0.64	−3.34	<0.01
	hurricane incidence	−0.23	−1.18	>0.05
2	size class	−0.35	−1.90	>0.05
	constant		8.55	<0.001
	shelf area	−0.73	−4.05	<0.01
3	size class	−0.28	−1.59	>0.05
	constant		8.64	<0.001
	shelf area	−0.76	−3.40	<0.01

Notes: Independent variables were entered backward. Results remained the same when independent variables were entered forward (Model 1 predictors: constant, size, shelf area, hurricanes. Model 2 predictors: constant, size, shelf area. Model 3 predictors: constant, shelf area). The dependent variable is N_g/N.

of clones was correlated with the degree of clonal propagation at the scale of individual reefs. Hence, on the within- and between-reef scale, clonal structure patterns were not predictable by any of the parameters that we assessed. Similar observations of highly variable contribution to asexual reproduction on fairly small spatial scales have been made for the dwarf eelgrass in the Black Sea (Coyer et al. 2004) and Californian sequoias (Douhovnikoff et al. 2004), although other studies have found uniform genotyptic richness over far larger spatial scales (e.g., Alberto et al. 2005).

Patterns in sexual contribution and genotypic diversity emerged on the scale of the two phylogeographic provinces. *Acropora palmata* populations in the western Caribbean appeared to have higher asexual recruitment rates, leading to lower genotypic diversity there than in the east (Table 3). The notable exception was Navassa, with its solely sexual populations and associated high genotypic diversities. This lack of clonal reproduction at Navassa is likely related to its exceptionally small shelf area (see *Discussion: Factors influencing asexual reproduction of populations*).

Despite the prevalence of asexual reproduction in the western Caribbean, overall colony density within surveyed areas was lower than in the eastern Caribbean (Table 3). Achieving higher population densities in the east with less asexual reproduction is unexpected because *A. palmata* is thought to have low rates of (sexual) larval settlement (Dustan 1977, Bak and Engel 1979, Hughes and Jackson 1980, 1985, Rylaarsdam 1983, Rosesmyth 1984). This suggests that sexual recruitment success in the eastern province has been quite high; perhaps even higher than for asexual recruitment in the west.

Factors influencing asexual reproduction of populations

Small-scale patterns of clonal variation within cnidarian species have been attributed to disturbance (Hunter 1993, Karlson et al. 1996, Coffroth and Lasker 1998b). Small-scale disturbance events such as waves generated from local storms may play an important role in influencing clonal structure. However, no Caribbean-wide datasets exist that would allow us to evaluate their influence on *Acropora palmata* stands. Hurricanes have frequent impacts on some reefs in both regions, while other localities like Curaçao, Bonaire, and Panama rarely lie in the path of destruction (Goldenberg et al. 2001). If hurricane frequency were the main cause underlying observed variation in clonal structure, then regions with low hurricane frequency should exhibit similarly low levels of asexual reproduction. This was not the case. Overall, our stepwise regression analysis indicated hurricane incidence explained little of the variation in clonal structure (Table 4, Fig. 6).

Theoretical work shows that hurricanes do not always lead to increased population sizes through fragment generation. Lirman's (2003) stage model of *Acropora palmata* predicted that when storm frequency increases over a certain threshold (once every two years), fragmentation may come at considerable cost to the colonies, leading to overall population decline especially when sexual input is limited. Apart from having a negative effect on growth rates and survivorship potential, sexual reproduction is depressed in both the surviving fragments and the source colony (Lirman 2000*a*). Similar results were observed for pacific acroporids in field manipulations (Smith and Hughes 1999).

Other studies show that both the magnitude and recency of disturbance affect genotypic diversity (Douhovnikoff et al. 2005, Travis and Hester 2005). In corals, highly asexual populations of *Porites compressa* in Hawaii had experienced recent severe disturbance, while populations dominated by sexual reproduction had been undisturbed for longer periods (Hunter 1993). A correlation between the clonal diversity (measured as G_o/G_e) and disturbance was also found for the Caribbean gorgonian *Plexaura kuna* (Coffroth and Lasker 1998*b*). However, in this case, intermediate levels of disturbance were correlated with the highest clonal diversity (see also Reusch 2006 for an example in seagrasses). Our data show neither a linear response to large-scale disturbance incidence nor an increase in clonal diversity (or richness or evenness) at intermediate levels of large-scale disturbance (Fig. 6).

Abiotic disturbance is a necessary but not sufficient condition for successful fragmentation (Coffroth and Lasker 1998*b*). Other requirements include the presence of large colonies in the population to provide the source of fragments and, depending on the severity of the disturbance, a topography that will retain the fragments within that population. Stepwise regression (Table 4, Fig. 6) supported the importance of habitat area and, to a much lesser extent, the size structure of the population. The narrow shelf surrounding Navassa may help explain the lack of successful clonal reproduction seen there relative to other populations in the western Caribbean (Fig. 6). *Acropora* fragments are likely generated by the high wave energy characteristic of this island, but its narrow shelf offers poor retention potential. Congruently, lower survival of artificially produced fragments of Pacific acroporids was evident on reef slopes compared to reef flats (Smith and Hughes 1999). Habitat area measured as slope may also be an index of other influential habitat characteristics such as the geomorphology of the area (volcanic, bank, shelf) and, consequently, sedimentation, freshwater influence, and other related factors.

Sexual recruitment may drive geographic patterns of clonal population structure

Factors influencing sexual rather then asexual recruitment may drive geographic patterns of clonal population structure in *Acropora palmata*. Note that here, sexual recruitment refers to when individuals have become part of the adult population (and we can

measure them), not to just the recruitment of larvae to the substrate (albeit the latter is a necessary first step). Genotypic richness was significantly higher in the eastern than in the western Caribbean, likely indicating higher sexual recruitment rates in the east (Coffroth and Lasker 1998*b*). For example, the Florida reefs dominated by only one clone have apparently had no sexual recruitment over the past few years. Studies of flowering plants have likewise found reliance on asexual reproduction at the geographic periphery of species' ranges (see Dorken and Eckert 2001).

Direct quantification of sexual recruitment in *A. palmata* over a large geographical scale is clearly needed but is difficult to do. Despite the large potential number of larvae produced each year, larval settlers of *A. palmata* have rarely been observed (Dustan 1977, Bak and Engel 1979, Hughes and Jackson 1980, 1985, Rylaarsdam 1983, Rosesmyth 1984). Similarly, successful recruitment of sexually produced seedlings is rare in riparian cottonwood species that mostly maintain their populations by asexual reproduction (Bradley and Smith 1986). Field assessments of sexual recruitment based solely on counts of small (<5 cm) *A. palmata* colonies of certain morphology are insufficient, because neither colony size nor morphology does reliably indicate sexual origin (M. W. Miller, I. B. Baums, and D. E. Willimas, *unpublished manuscript*).

Support for the hypothesis of sexual recruitment as the driving factor of clonal structure in acroporid corals comes from other studies. Along the Great Barrier Reef (GBR), *Acropora valida* and *A. millepora* show similar variation in values of N_g/N and G_o/G_e among sites within a reef (hundreds of meters [Ayre and Hughes 2000]) as observed here for *A. palmata* in the Caribbean. Levels of sexual larval input might be an important structuring force in reef communities: Connell et al. (1997) showed that over 30 years, coral larval recruitment patterns varied 7.5-fold among sites within one of Ayre and Hughes's study reefs. In addition, a regional pattern in clonal structure emerged for *A. valida* that was attributed to gradients in larval recruitment along the GBR (Hughes et al. 2000). Interestingly, this variation in acroporid larval recruitment was ascribed largely to differences in fecundity of adults, not their abundance (Hughes et al. 2000).

Consequences of variation in clonal structure

For clonal species, the number of breeding genets (not ramets) will set an upper bound on the effective population size. In *A. palmata*, approximately half of the individual colonies sampled represented distinct genets, although this average proportion was smaller in the western than the eastern phylogeographic province (Table 3). Large clones might contribute disproportionately to a population's reproductive output (Hammerli and Reusch 2003), but extensive cover by a single clone could also limit the output of larvae in an obligately outcrossing species like *A. palmata* (Davis et al. 2004, Baums et al. 2005*a*). Populations with small effective population sizes are more prone to extinction due to demographic stochasticity, reduction in gene diversity, or accumulation of deleterious mutations (Ellstrand and Elam 1993, Grosberg and Cunningham 2000).

In asexually reproducing species, population maintenance via clonal propagation can allow for persistence of populations during times of reduced sexual recruitment (i.e., a buffer to demographic stochasticity [Lasker and Coffroth 1999]). In Florida, asexual proliferation of clones has allowed populations to thrive at reefs with only one genet each. One additional stand in Biscayne National Park, Florida (Boomerang Reef, 25°21′10″ N, 80°10′41″ W) was subsequently found to be monoclonal over similar spatial scales (data not shown, $n = 12$). For external fertilizers, once the densities of individuals, specifically that of non-clone-mates, becomes so low that dilution of gametes is too great for fertilization to occur (Allee effect; see Pennington 1985, Knowlton 1992, Levitan 1992, Coffroth and Lasker 1998*a*, Davis et al. 2004), sexual reproductive success is decreased even further. Such remnant populations may become sexually extinct after prolonged clonal growth and absence of immigration from other populations (ecologically driven extinction, Honnay and Bossuyt 2005). Sexual extinction becomes more likely in fragmented populations and in populations at the extremes of the species' range due to decreases in the frequency of immigration (Ellstrand and Roose 1987, Eckert 2002, Honnay and Bossuyt 2005). Data consistent with this pattern was presented for corals from the Great Barrier Reef (Ayre and Hughes 2004). Thus, while monoclonal populations, such as some of the Florida *A. palmata* stands, enable the persistence of the species in a particular patch and thereby preserve some of the genetic diversity of the species, these populations exhibit an extinction debt (sensu Honnay and Bossuyt 2005).

There is mounting evidence that genotypic diversity of structural species may fulfill a similar role as species diversity in whole ecosystems, conferring resilience to disturbance (Reusch et al. 2005). An important factor that led to the decline of *Acropora palmata* populations in the Caribbean was the outbreak of the acroporid-specific White Band Disease. Different genets may show differential susceptibility to the disease. Genets of another reef-building coral, *Montastraea franksi*, have been shown to be differentially susceptible to bleaching (Edmunds et al. 2003). Thus, *A. palmata* populations with high genet diversity, as in the eastern Caribbean, are more likely to withstand future threats such as emerging diseases or global change (Lasker and Coffroth 1999) than populations with low genet diversity, like most of those in the western Caribbean. Conversely, massive regional disease impacts in the recent past may have influenced the genotypic structure observed in the present study, but this is impossible to quantify.

Despite dramatic decline in *A. palmata* abundance, no genetic signature of a bottleneck was evident in our data set. Formal analysis with the program BOTTLENECK (Piry et al. 1999) did not detect excess gene diversity over expected gene diversity under mutation-drift equilibrium when assuming an infinite allele model (IAM) or a stepwise mutation model (SMM) for our microsatellite markers regardless of the test statistic used (data not shown). The long life spans of genets in this species may buffer against loss of genetic diversity for some time after severe population reductions (Appendix C). In general, genetic diversity in asexually reproducing species is expected to be comparable to solely sexually reproducing species as long as sexual reproduction occurs at least occasionally in the former (Bengtsson 2003, Halkett et al. 2005).

The depressed status of acroporid populations in the Caribbean has led to their impending listing as threatened under the U.S. Endangered Species Act. Because the eastern and western *Acropora palmata* populations appear to differ in their genotypic diversity and may differ demographically (i.e., vary in the relative importance of sexual and asexual recruitment), conservation strategies need to be tailored to local conditions. Due to self-incompatibility, only stands where neighboring spawners are of distinct genotypes (assuming gamete dispersal distances are modest relative to the spatial extent of large clones, Coffroth and Lasker 1998*a*) can serve as effective larval sources for surrounding populations. These diverse stands are more likely to harbor genotypes that may be resistant against future disease outbreaks. Hence, the substantial geographic variation in genotypic diversity demonstrated here implies large variation in the expected capacity of individual populations to persist and recover.

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APPENDIX A

Photographs depicting the varying morphology of *Acropora palmata* colonies, from plating to branching to encrusting (*Ecological Archives* M076-019-A1).

APPENDIX B

Representative polar plot maps of genotypic diversity within populations of *Acropora palmata* (*Ecological Archives* M076-019-A2).

APPENDIX C

Gene diversity of *Acropora palmata* estimated based on two data sets: one including only unique multilocus genotypes (genets) and one including all samples (all genotypes) (*Ecological Archives* M076-019-A3).