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Restricted Gene Flow in the Caribbean Staghorn Coral *Acropora cervicornis*: Implications for the Recovery of Endangered Reefs

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Abstract

Coral reef conservation requires information about the distance over which healthy reefs can rescue damaged reefs through input of coral larvae. This information is desperately needed in the Caribbean where the 2 dominant shallow water corals *Acropora cervicornis* and *Acropora palmata* have suffered unprecedented declines. Here we compare the population genetic structure in the staghorn coral *A. cervicornis* across the greater Caribbean using DNA sequence data from 1 mitochondrial and 3 nuclear genes. Data from 160 individuals from 22 populations and 9 regions show that *A. cervicornis* exhibits significant population genetic structure across the greater Caribbean in both the mitochondrial ($\Phi_{st} = 0.130$) and nuclear data ($\Phi_{st} = 0.067$). The highest population structure was observed in the species' own, native mtDNA haplotypes ($\Phi_{st} = 0.235$). Introgressed alleles from *A. palmata* tempered higher population structure in *A. cervicornis* over regional scales but in some cases generated highly localized "introgression hot spots" and fine-scale genetic structure among reefs separated by as few as 2 km. These data show that larval dispersal over moderate or long distances (>500 km) is limited for this threatened species and in some cases locally limited as well. Thus, the endangered Caribbean staghorn corals require local source populations for their recovery and targeted conservation efforts over spatial scales much smaller than the hundreds to thousands of kilometers usually proposed for marine reserves.

Coral reefs have suffered global declines due to climate change, coral bleaching, overfishing, habitat destruction, disease, and other anthropogenic factors (Hughes et al. 2003; Pandolfi et al. 2003). These declines have been particularly dramatic on Caribbean reefs (Gardner et al. 2003) due to historical overfishing (Hughes 1996; Jackson et al. 2001), the mass mortality of an important sea urchin (Lessios 1988), and the unprecedented decline of *Acropora* corals due to white-band disease (Gladfelter 1982; Aronson and Precht 2001). Because corals as architectural species are key to the persistence and stability of thousands of other species (Knowlton 2001), the future of reef communities depends on the ability of reef corals to respond to increasing climate change and human disturbance (Hughes et al. 2003). An impediment to understanding how corals will respond to ecological perturbation has been poor knowledge about the demographic and evolutionary connections among coral populations over broad spatial scales. Are coral populations interconnected by high gene flow such that disturbed reefs can be replenished by long-distance dispersal? Recent genetic evidence from Pacific corals (Ayre and Hughes 2000, 2004) and the Caribbean coral *Acropora palmata* (Baums et al. 2005) show low to moderate gene flow among reefs separated by 500 km, implying limited ability of reefs to seed one another over large distances. If this is true, then the widely separated coral reefs of the world represent a mosaic of management tiles all requiring individual conservation plans.

Recent and rapid declines of the Caribbean *Acropora* corals due to white-band disease (Aronson and Precht 2001) and other factors (Knowlton et al. 1981; Woodley et al. 1981; Porter et al. 1982; Cortez 1994) underscore the need to understand how reef corals are genetically interconnected by larval dispersal. Losses of these 2 dominant shallow water Caribbean corals (Goreau 1959) exceed 95% in many locations (Bak and Criens 1982; Jaap et al. 1988; Aronson and Precht 1997, 2001; Miller et al. 2002), and as a result, both

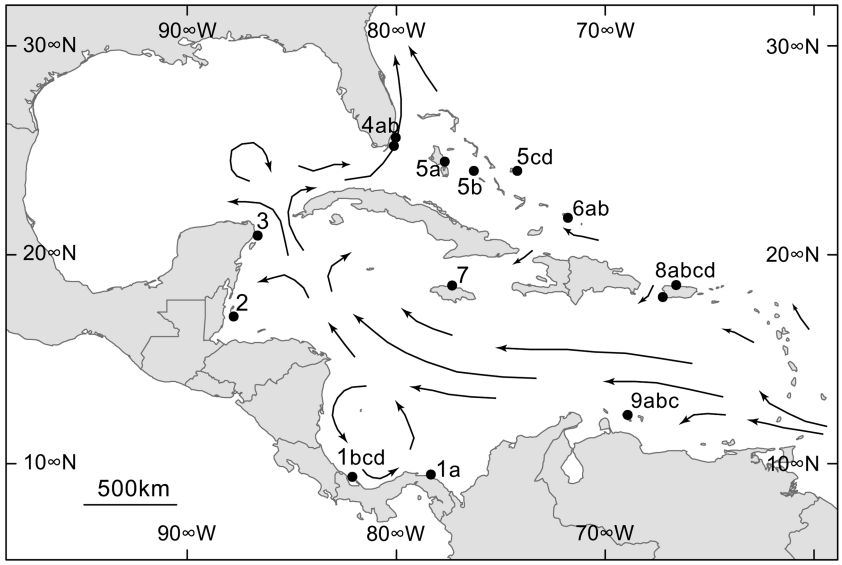

Figure 1. Collection localities from 9 regions in the Caribbean, and Bahamas, and Florida with the major surface currents (Wust 1964). (1) Panama—a. San Blas, b. Salt Creek, c. Crawl Cay, and d. Casa Blanca (Bocas del Toro); (2) Belize; (3) Yucatan; (4) Florida—a. Florida Keys, b. Fort Lauderdale; (5) Bahamas—a. Andros Island, b. Lee Stocking Island, c. North San Salvador Island, and d. Southwest San Salvador Island; (6) South Caicos, Turks and Caicos—a. *Montastraea* Reef, b. Patch Reef; (7) Discovery Bay, Jamaica; (8) Puerto Rico—a. San Juan, b. San Cristobal, c. Media Luna, d. Guanica; (9) Curacao—a. Jan Thiel, b. Fuik, c. Spaanse Water.

species have recently been listed as threatened under the Endangered Species Act in the United States (Diaz-Soltero 1999; Precht et al. 2002). The poor recovery of *Acropora cervicornis*, in particular, has been attributed to its heavy reliance on asexual fragmentation (Tunnicliffe 1981; Highsmith 1982; Neigel and Avise 1983) and rare sexual recruitment (Bak and Engel 1979; Tunnicliffe 1981; Knowlton et al. 1990; Vargas-Angel et al. 2003). Although *A. cervicornis* can recover locally by asexual fragmentation, recolonization of lost habitat will have to be achieved by larval dispersal. Thus, information about the population genetic structure of *A. cervicornis* is vital to conservation management. Recently published microsatellite data show that gene flow is restricted in the congener *A. palmata*, especially between the Western and Eastern Caribbean (Baums et al. 2005). Is long-distance gene flow uncommon in *A. cervicornis* as well?

Here we compare the population genetic structure of *A. cervicornis* across the greater Caribbean using DNA sequence data from 1 mitochondrial and 3 nuclear genes. Previous genetic work has shown that *A. cervicornis* hybridizes with its sympatric congener *A. palmata* (van Oppen et al. 2000; Vollmer and Palumbi 2002) and receives genes from *A. palmata* through rare, one-way introgression (Vollmer and Palumbi 2002). These introgressed genes complicate population genetic analyses because they can enter populations by crossing the species boundary and via gene flow between populations. We show here that *A. cervicornis* exhibits moderate to high levels of population structure among regions separated by more than 500 km and thus requires local management and conservation. We also show that introgressed genes in some cases can generate fine-scale genetic structure over spatial scales as small as 2 km.

Materials and Methods

Acropora cervicornis was collected from 22 locations spanning 9 regions in the Caribbean, Florida, and Bahamas (Figure 1, Table 1). Corals were sampled at least 5 m apart to reduce the collection of asexual clonemates, preserved in 95% ethanol and stored at room temperature. Ten or more corals were sampled from each population whenever possible; however, at some of our study sites, there were few remaining *A. cervicornis*, and this is reflected in our sample.

DNA was isolated using a cetyltrimethylammonium bromide buffer, proteinase K (100 μg), and standard phenol–chloroform extraction methods. Amplifications were obtained for the mitochondrial (mtDNA) control region (van Oppen et al. 1999) and 3 single-copy nuclear genes (MiniCollagen, Calmodulin, and *Pax*C) using coral-specific primers and GeneAmp XL polymerase chain reaction (PCR) kits under normal PCR conditions, 30–35 cycles, annealing temperatures of 51–54 °C, and extension times up to 2 min. The mitochondrial control region (941 bp) was amplified and sequenced using the PCR primers CRf and CO3r and internal sequencing primers CRseqf and CRseqr (Vollmer and Palumbi 2002). A 373-bp fragment of Mini-Collagen including the second intron was amplified using published primers (Wang et al. 1995). A calmodulin intron (334 bp) was amplified with the primers CalMf and CalMr2 (Vollmer and Palumbi 2002). A *Pax*C intron (516 bp)

Table 1. Collection localities by region with the number of samples, unique individuals (i.e., genets), and the ratio of samples to genets listed by population and region

Region	Population	No. of samples	No. of genets	Genets/ ramets
1. Panama		38	25	0.658
	a. San Blas	7	5	0.714
	b. Salt Creek, Bocas del Toro	11	9	0.818
	c. Crawl Cay, Bocas del Toro	10	8	0.800
	d. Casa Blanca, Bocas del Toro	10	3	0.300
2. Belize		31	12	0.387
3. Yucatan		3	3	1.000
4. Florida		15	5	0.333
	a. Florida Keys	7	3	0.429
	b. Ft. Lauderdale	8	2	0.250
5. Bahamas		52	33	0.635
	a. Andros Island	21	7	0.333
	b. Lee Stocking Island	8	6	0.750
	c. North San Salvador Island	10	7	0.700
	d. Southwest San Salvador Island	13	13	1.000
6. Turks and Caicos		51	33	0.647
	a. *Montastraea* Reef, South Caicos	37	22	0.595
	b. Patch Reef, South Caicos	14	11	0.786
7. Jamaica		9	4	0.444
8. Puerto Rico		48	26	0.542
	a. San Juan	4	4	1.000
	b. San Cristobal, La Parguera	18	11	0.611
	c. Media Luna, La Parguera	13	6	0.462
	d. Guanica	12	5	0.417
9. Curacao		30	19	0.633
	a. Jan Thiel	10	6	0.600
	b. Fuik	10	7	0.700
	c. Spaanse Water	10	6	0.600
Total		276	160	0.580

was amplified using published primers (van Oppen et al. 2000). PCR amplifications were sequenced directly using ABI BigDye cycle (Applied Biosystems, Foster City, CA) sequencing chemistry and analyzed with automated DNA sequencers (ABI model 377 and 3100). Heterozygous nuclear alleles were observed as double peaks confirmed in samples sequenced in both directions and identified using diploid sequencing techniques (Hare and Palumbi 1999). Nuclear alleles were identified in homozygous individuals and/or by cloning low-frequency nuclear alleles from heterozygous individuals. Allelic compositions of heterozygotes were easily resolved due to the low numbers of nuclear alleles per locus. Multilocus genetic data were used to genotype corals and identify clones produced by asexual fragmentation. Putative clones could be identified with a high probability of identity ($P = 0.002$) and were excluded from all analyses to prevent biasing allele frequencies.

Maximum likelihood (ML) phylogenies were constructed using PAUP* 4.0b10 (Swofford 1996) with estimated model parameters and 25 random-addition heuristic searches with tree-bisection-reconnection branch swapping using sequence data from *A. cervicornis*, its congener *A. palmata*, and the hybrid *A. prolifera*. Models of sequence evolution were evaluated on distance-based topologies with hierarchical likelihood ratio tests in MODELTEST 3.06 (Posada and Crandall 1998). Two informative gaps in the mitochondrial control region and a 13-bp deletion in *Pax*C (allele Pax_i3) were coded as single base changes. Native and introgressed allele clades were identified using ML phylogenies and Bayesian coalescent analyses (Nielsen and Wakeley 2001; Hey and Nielsen 2004) as outlined in Vollmer and Palumbi (2002). Our previous work showed that the mtDNA and *Pax*C data were consistent with rare, one-way gene flow (Vollmer and Palumbi 2002). Further coalescent modeling using the program IM (Hey and Nielsen 2004), which allows for bidirectional gene flow estimates between species, indicates that the shared allele in Calmodulin is also consistent with one-way interspecific gene flow (Vollmer SV, Palumbi SR, unpublished data). These coalescent results combined with a clear phylogenetic pattern of one-way gene flow from the congener *A. palmata* to *A. cervicornis* (Vollmer and Palumbi 2002) allow us to identify alleles in *A. cervicornis* derived from hybridization with *A. palmata*. All 4 gene trees have 2 allele clades—one that is exclusive to *A. cervicornis* and a second clade containing both *A. cervicornis* and *A. palmata*. The allele clade found exclusively in *A. cervicornis* represents native alleles, whereas the second shared allele clade represent *A. palmata* alleles that are introgressed in *A. cervicornis*.

Population genetic structure was estimated using analysis of molecular variance (AMOVA) in ARLEQUIN 2.0 (Schneider et al. 2000). Hierarchical AMOVA was used to estimate levels of genetic differentiation among populations (Φ_{st}), between regions (Φ_{ct}), and between populations within regions (Φ_{sc}). AMOVA was conducted for the complete mtDNA data set and then independently for the native mtDNA data (i.e., only putative *A. cervicornis* haplotypes). The introgressed mtDNA data were not compared separately due to low sample sizes. AMOVA was also conducted for the complete nuclear data set and independently for the 3 nuclear loci. Pairwise Φ_{st} values were calculated to estimate genetic differentiation among regions, and P values were adjusted using sequential Bonferroni techniques (Sokal and Rohlf 1995).

Within each region, small-scale genetic differentiation among reefs less than 100 km apart was tested using Hudson's (2000) nearest neighbor statistic (S_{nn}) implemented in the program DNASP 4.0 (Rozas et al. 2003) and estimated using the F_{st} of Hudson et al. (1992) for each gene separately. Many of these small-scale comparisons are among reefs with fewer than 10 genets, which partially reflects the biological reality that there are often few genets on individual reefs. Low samples sizes should reduce our power to detect fine-scale structure, but in some case it may also give the

appearance of strong genetic differentiation. To account for the effect of multiple comparisons and small samples sizes, *P* values of the S_{nn} statistics were adjusted using sequential Bonferroni techniques based on the number of regions compared per gene; however, these Bonferroni corrections did not modify the interpretations of fine-scale differentiation. Exact tests were used to detect deviations from Hardy–Weinberg expectations (HWE) and linkage disequilibrium across loci using GENEPOP 1.2 (Raymond and Rousset 1995). All populations conformed to HWE, and all loci were in linkage equilibrium (results not shown). Absence of linkage disequilibrium suggests that introgressed genes are not strongly linked or bound up in recent generation backcross individuals (Vollmer SV, Palumbi SR, unpublished data).

Results

Multilocus sequence data from the mitochondrial (mtDNA) control region and 3 nuclear genes (MiniCollagen, Calmodulin, and *Pax*C) were obtained from 276 colonies of *A. cervicornis* spread across 22 populations from 9 regions in the Caribbean, Florida, and Bahamas (Figure 1, Table 1). A total of 160 corals (or 58% of the entire sample) were identified as unique individuals or genets (Table 1) based on the multilocus genotype data from one or more loci. The ratio of genets to samples did not differ between regions ($\chi^2 = 4.08$, df = 8, $P = 0.850$) or among populations ($\chi^2 = 11.68$, df = 21, $P = 0.948$). The highest numbers of individuals (ca. 20+) were obtained from 5 widespread regions: Panama, Bahamas, Turks and Caicos, Puerto Rico, and Curacao. Belize had 12 individuals, but only mtDNA sequences were obtained due to poor sample preservation. Genetic analyses were conducted using data from all 22 populations across the 9 regions. Three regions (the Yucatan, Florida, and Jamaica) were excluded from pairwise regional comparisons due to small sample sizes.

ML phylogenies for all 4 genes (Figure 2) were characterized by having 2 clades of alleles—one representing native *A. cervicornis* alleles (i.e., the species' own alleles) and the other composed of introgressed alleles (shown in gray) derived from one-way gene flow from *A. palmata* (Vollmer and Palumbi 2002). The mitochondrial control region had the highest number of alleles/haplotypes with a total of 27 haplotypes being observed in *A. cervicornis*, 15 native haplotypes and 12 introgressed haplotypes. Haplotype diversity (h_d) and nucleotide diversity (π) measured 0.847 and 0.0057, respectively, in the mitochondrial data, including introgressed haplotypes, and 0.780 and 0.0023 in the native mitochondrial haplotypes. The 3 nuclear genes had fewer alleles. Three alleles were observed at MiniCollagen ($h_d = 0.369$; $\pi = 0.0010$), of which all were native alleles. Three alleles were observed at Calmodulin ($h_d = 0.423$; $\pi = 0.0075$), 2 native alleles and 1 introgressed allele. Four alleles were observed at *Pax*C ($h_d = 0.385$; $\pi = 0.0016$), 1 native allele and 3 introgressed alleles. Average heterozygosities for the 3 nuclear genes across the 9 regions were 0.194 for MiniCollagen, 0.405 for Calmodulin, and 0.359 for *Pax*C.

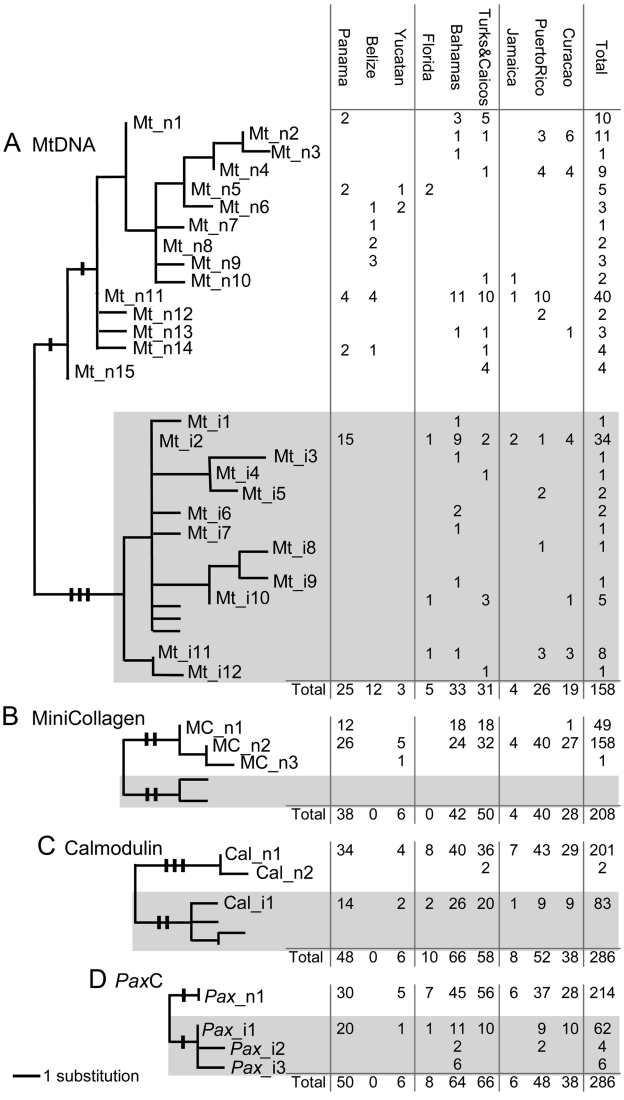

Figure 2. ML trees for (**A**) mitochondrial control region (Mt), (**B**) MiniCollagen (MC), (**C**) Calmodulin (Cal), and (**D**) *Pax*C (*Pax*) showing the geographic distribution of alleles across 9 regions in the Caribbean, Bahamas, and Florida. Native alleles are in white and introgressed alleles are highlighted in gray (from Vollmer SV, Palumbi SR, in preparation). Alleles found in *Acropora cervicornis* are labeled and coded with a gene abbreviation (e.g., MiniCollagen as MC) and a code for whether it was native (n) or introgressed (i). Unlabeled branch tips represent alleles that were observed in *Acropora palmata* or hybrid *A. prolifera*, but not *Acropora cervicornis*. Tick marks along major branches indicate substitutions. (**A**) MtDNA ML tree constructed using a general time reversible + Γ + I model (1 of 6 trees, ln score = 1537.7). (**B**) MiniCollagen ML tree constructed using a Jukes-Cantor model (ln score = 575.7). (**C**) Calmodulin ML tree constructed using a GTR model (ln score = 477.9). (**D**) *Pax*C ML tree constructed using an F81 model (ln score = 733.7). Sequences are available on GenBank.

Table 2. AMOVA results showing levels of genetic structure between populations within regions (Φ_{sc}), between populations (Φ_{st}), and between regions (Φ_{ct}). Mitochondrial DNA included native and introgressed genetic variation, and Native mtDNA included only putative *Acropora cervicornis* haplotypes. Nuclear DNA was analyzed together and separately for each gene—MiniCollagen, Calmodulin, and *Pax*C

Gene	Φ_{sc}	Φ_{st}	Φ_{ct}
Mitochondrial DNA	0.016	0.130**	0.100*
Native mtDNA	−0.018	0.235**	0.249**
Nuclear DNA	0.041	0.067**	0.027
MiniCollagen	0.025	0.189**	0.167*
Calmodulin	0.013	0.021	0.008
*Pax*C	0.075*	0.075**	−0.001

* $P < 0.05$, ** $P < 0.001$.

Acropora cervicornis exhibited significant population structure across the greater Caribbean (Table 2) in both the mtDNA ($\Phi_{st} = 0.130$, $P = 0.0006$) and nuclear ($\Phi_{st} = 0.067$, $P = 0.0012$) data sets. At the regional level, significant population structure was detected in the complete mtDNA data ($\Phi_{ct} = 0.100$, $P = 0.027$) but not in the nuclear data. Overall, the highest population structure was detected in the native mtDNA data, both among populations ($\Phi_{st} = 0.235$, $P = 0.00001$) and between regions ($\Phi_{ct} = 0.249$, $P = 0.00001$). Thus, the removal of introgressed haplotypes in the mitochondrial data (mtDNA vs. native mtDNA, Table 2) resulted in more than a 2-fold increase in the genetic structure among regions (Φ_{ct}) and a comparable increase in the genetic structure among populations (Φ_{st}). In the nuclear genes, highest population structure was observed at MiniCollagen, both among populations ($\Phi_{st} = 0.189$, $P = 0.007$) and regions ($\Phi_{ct} = 0.167$, $P = 0.010$), which reflects only differences in native variation. At *Pax*C, lower but significant genetic structure was detected among populations ($\Phi_{st} = 0.075$, $P = 0.003$) but not among regions. Because there is only one native allele at *Pax*C, this observed population structure among populations ($\Phi_{st} = 0.075$) resulted from variation in the frequencies of introgressed alleles and between introgressed versus native alleles. No significant population structure was detected with Calmodulin.

Pairwise comparisons among regions showed significant and often high levels of genetic structure between the 6 well-sampled regional populations (Table 3) such that regional populations separated by more than 500 km were genetically differentiated. Pairwise Φ_{st} values averaged (±SE) 0.124 ± 0.032 in the complete mtDNA data set and 0.176 ± 0.039 in the native mtDNAs. Three regions—Curacao, Belize, and Panama—stand out as particularly distinct. For Curacao and Belize, high pairwise Φ_{st} values were observed in both the complete and native mtDNA data. In Panama, high pairwise Φ_{st} values were observed predominantly in the complete mtDNA data and reflect the high frequency of introgressed mtDNA in Panama (60%). Pairwise Φ_{st} values averaged (±SE) 0.060 ± 0.016 in combined nuclear data and 0.174 ± 0.052 at MiniCollagen (lower diagonal, Table 3). Highest pairwise Φ_{st} values in the nuclear data were observed between 2 groups—Panama, Bahamas, and the Turks and Caicos versus Puerto Rico and Curacao—and were driven by frequency differences in native MiniCollagen alleles.

On the gene trees, phylogeographic patterns were consistent with the regional differences in population structure (Figure 2). The most common native mtDNA (Mt_n11), which was found in every well-sampled region at an overall frequency of 25%, was absent in Curacao, indicating little larval input from outside populations. There was also evidence for the distinctiveness of the Western Caribbean (i.e., Panama, Belize, and the Yucatan) and a possible genetic connection between the Western Caribbean and Florida. In particular, 2 geographically restricted haplotypes (Mt_n5 and Mt_n6) were detected in the Western Caribbean, one of which (Mt_n5) was also found in 2 out of the 5 Florida samples. Additional sampling would be required to substantiate this Western Caribbean/Florida connection. Belize was also distinctive possessing 4 mtDNA haplotypes that were endemic (Mt_n7, n8, n9) or observed only in the Western Caribbean (Mt_n6). Phylogeographic patterns were less apparent on the nuclear gene trees due in part to the low number of alleles. At MiniCollagen, the MC_n1 allele was at relatively high frequency in Panama, Bahamas, and Turks and Caicos but rare

Table 3. Pairwise Φ_{st} between regional populations. Upper diagonal (in gray) calculated from mitochondrial and nuclear data sets including introgressed alleles. Lower diagonal calculated from native alleles, that is, native mtDNA haplotypes and MiniCollagen alleles, respectively

	Mitochondrial DNA						Nuclear genes					
	1	2	3	4	5	6	1	2	3	4	5	6
1. Panama		**0.434**	0.001	**0.216**	**0.181**	0.093*		N/A	0.024	0.047*	**0.092**	0.039
2. Belize	0.044		**0.284**	0.110*	0.097*	0.227*	N/A		N/A	N/A	N/A	N/A
3. Bahamas	0.053	**0.210**		0.083*	0.068	0.025	0.002	N/A		0.002	**0.140**	**0.089**
4. Turks and Caicos	−0.009	0.124*	−0.017		−0.024	0.066	−0.019	N/A	−0.012		**0.115**	0.064*
5. Puerto Rico	0.106	**0.177**	0.104*	0.087*		0.006	**0.304**	N/A	**0.408**	**0.321**		−0.012
6. Curacao	**0.338**	**0.364**	**0.477**	**0.369**	0.213*		**0.195**	N/A	**0.304**	0.226*	0.013	

Values in bold are those that are significant after sequential Bonferroni adjustment; N/A = no nuclear data from Belize; *P value < 0.05 before correction.

or absent in the other well-sampled populations, that is, Curacoa and Puerto Rico. There was also evidence of restricted dispersal in an introgressed *Pax*C allele (Pax_i3), which was observed in multiple populations in the Bahamas but nowhere else (Figure 2, Appendix 1).

Fine-scale genetic differentiation among reefs (separated by less than 100 km) was observed in 3 out of 20 comparisons in 3 regions (Puerto Rico, Bahamas, and Panama) and 2 genes (MtDNA and *Pax*C). This indicates that fine-scale population structure can occur over spatial scales of less than 100 km but that it does so rarely. These fine-scale genetic differences are interesting because in each case they were due to highly localized introgression signatures at a single reef (Appendix 1). In Puerto Rico, the high frequency of an introgressed *Pax*C_i1 allele at Media Luna (75%) drove a strong signature of local genetic differentiation among 3 reefs ($F_{st} = 0.344$, $S_{nn} = 0.507$, $P < 0.0001$) including 2 reefs—Media Luna and San Cristobal—separated by only 2 km ($F_{st} = 0.476$, $P = 0.0001$). In San Salvador, northern and southwestern populations differed at *Pax*C ($F_{st} = 0.103$, $P = 0.009$) and possessed different sets of introgressed *Pax*C variants. Both populations also showed genetic structure at Calmodulin ($F_{st} = 0.155$, $S_{nn} = 0.570$, $P = 0.015$) due to high frequencies of introgressed Calmodulin alleles in the north. In Panama, significant differences were detected in the mtDNA data among 3 reefs in Bocas del Toro ($F_{st} = 0.315$, $S_{nn} = 0.591$, $P = 0.002$) including 2 reefs—Salt Creek and Crawl Cay—separated by approximately 2 km ($F_{st} = 0.158$, $P = 0.004$). These 2 reefs shared no native haplotypes and differed in the frequency of introgressed mtDNA haplotypes (33% vs. 75%, respectively).

Discussion

Our multilocus genetic data show that the staghorn coral *A. cervicornis* exhibits significant population structure across the greater Caribbean in both the mitochondrial and nuclear loci. Moderate levels of population genetic structure observed in both the mitochondrial and nuclear data sets indicate that regional populations separated by more than 500 km are genetically differentiated and require independent conservation and management. In particular, the high levels of population genetic structure observed in the native mitochondrial data set ($\Phi_{st} = 0.235$) indicates that gene flow (*Nm*) across the greater Caribbean is low in *A. cervicornis* (Wright 1951). Fine-scale genetic differences among reefs separated by as little as 2 km suggest that gene flow may be limited over much smaller spatial scales as well.

Even though significant population genetic structure was detected in the mtDNA and nuclear data sets, there were pronounced differences in the estimated population structure between genes and in comparisons between data sets including introgressed alleles and data sets restricted to native alleles (i.e., the species' own alleles). Although some of this variation can be attributed to differences in the allelic diversity between genes (i.e., many mtDNA haplotypes vs. few nuclear alleles), the largest effect on the estimated population structure in *A. cervicornis* was due to introgressed alleles, which tempered higher native population structure over regional scales but in some cases generated additional population genetic structure over smaller spatial scales. For example, the removal of introgressed haplotypes in the mitochondrial data (thus leaving only native mtDNA variation) resulted in a more than 2-fold increase in the regional genetic structure (Φ_{ct}, Table 2). Whereas, at the *PaxC* nuclear gene, frequency differences between introgressed and native alleles generated genetic structure among populations (Φ_{st}) but not among regions (Φ_{ct}, Table 2).

Introgression of alleles from *A. palmata* represents a source of genetic variation for local populations of *A. cervicornis* that acts in addition to the typical population processes of mutation and migration. Like mutation, introgression can introduce new genetic variation into populations locally. Yet, unlike mutations, where polymorphisms are typically identical by descent, introgressed alleles (especially common variants) can cross the species boundary multiple times into different lineages and populations. Over broad spatial scales, these parallel introgression events mimic migration in population genetic analyses and give the appearance of increased genetic connectivity. For example, introgressed alleles Cal_i1 and *Pax*C_i1 occur in virtually all populations of *A. cervicornis* (Figure 2). Did these alleles introgress once from *A. palmata* and then spread by gene flow within *A. cervicornis*? Or did they introgress separately into different populations of *A. cervicornis*? In the former case, analysis of spatial patterns in introgressed alleles would reflect dispersal patterns within *A. cervicornis*. Whereas, in the latter case, spatial patterns of introgressed alleles would reflect a combination of factors including the phylogeographic structure in *A. palmata*, local patterns of interspecific hybridization and gene exchange (including selection against introgressed alleles), and dispersal of introgressed alleles among populations of *A. cervicornis*. High native population structure in the mitochondrial data and MiniCollagen among regions coupled with an absence of regional differences in introgressed alleles at *Pax*C or Calmodulin indicate that the patterns in introgressed alleles reflect both the local histories of interspecific gene flow and the restricted dispersal of introgressed variants between regional populations.

However, over smaller spatial scales such as adjacent reefs, our data show that introgressed alleles can contribute to fine-scale population structure by adding new genetic variation into local populations. This was apparent in the 3 cases of fine-scale genetic structure from Puerto Rico, San Salvador, and Panama where highly localized introgression signatures (i.e., introgression hot spots), often at a single gene, generated genetic structure over spatial scales as small as adjacent reefs (2–20 km). Although these introgression hot spots could result from different degrees of local hybridization, the absence of strong linkage disequilibrium among genes on these reefs indicates that recent hybrid and backcross generation individuals were not common in the samples (Vollmer SV, Palumbi SR, unpublished data). Thus, recent hybridization and backcrossing alone cannot account for the highly localized introgression hot spots. Therefore, it seems likely that these fine-scale differences reflect both the amount of past hybridization on reefs and changes in

Table 4. Summary of reef coral population genetic surveys and results

Species	Marker	Locations	Scale (km)	F_{st}	Significance	References
Indo-Pacific						
Acropora cuneata	Allozymes	GBR and Lord Howe	1900	0.24–0.34	Yes	1
	Allozymes	GBR	1200	0.05	No	2
Acropora cytherea	Allozymes	GBR	1200	0.03	Yes	2
Acropora hyacinthus	Allozymes	GBR	1200	0.05	Yes	2
Acropora millepora	Allozymes	GBR	1200	0.02	No	2
Acropora nasuta	Msats; intron	GBR	800	0.03	Yes	3
Acropora palifera	Allozymes	GBR	1200	0.02	No	2, 4
Acropora valida	Allozymes	GBR and Lord Howe	1900	0.19–0.25	Yes	1
	Allozymes	GBR	1200	0.02	No	2
Goniastrea aspera	Allozymes	Japan	500	0.03–0.10	Yes	5
Pleiastrea versipora	ITS rDNA	GBR and Japan	4000	N/A	Yes	6
Pocillopora damicornis	Allozymes	GBR and Lord Howe	1900	0.14–0.18	Yes	1
	Allozymes	GBR	1200	0.01	No	2, 4, 7
	Allozymes	Lord Howe	25	0.1	Yes	8
	Allozymes	Western Australia	400	0.39	Yes	9
	Allozymes	Japan	650	0.06	Yes	10
Pocillopora verrucosa	ITS rDNA	South Africa	70	0	No	11
Pocillopora meandrina	Msats	South Pacific	2000	0.11	Yes	12
Mycedium elephantotus	Allozymes	Taiwan	200	0.05	Yes	13
Seiatopora hystrix	Allozymes	GBR and Lord Howe	1900	0.03–0.41	Yes	1
	Allozymes	GBR	1200	0.15	Yes	2
	Msats	Red Sea	610	0.09; 0.14	Yes	14
Stylophora pistillata	Allozymes	GBR and Lord Howe	1900	0.09–0.18	Yes	1
	Allozymes	GBR	1200	0.09	Yes	2
	ITS rDNA	GBR to Japan	7000	0.12	N/A	15
Caribbean						
Acropora cervicornis	MtDNA; introns	Caribbean wide	2500	0.24	Yes	Here
Acropora palmata	Msats	Caribbean wide	2500	0.04; 0.15	Yes	16
Agaricia agaricities	AFLP	Bahamas and Florida	1000	0.07	Yes	17
Montastraea annularis	MtDNA; AFLPs	Bahamas and Panama	1500	0.24	Yes	18
Montastraea faveolata	MtDNA; AFLPs	Bahamas and Panama	1500	0.23	Yes	18
Montastraea franksi	MtDNA; AFLPs	Bahamas and Panama	1500	0.20	Yes	18

References: (1) Ayre and Hughes (2004); (2) Ayre and Hughes (2000); (3) Mackinzie et al. (2004); (4) Benzie et al. (1995); (5) Nishikawa and Sakai (2003); (6) Rodriguez-Lanetty and Hoegh-Guldberg (2002); (7) Ayre et al. (1997); (8) Miller and Ayre (2004); (9) Stoddart (1984); (10) Adjeroud and Tsuchiya (1999); (11) Ridgway et al. (2001); (12) Magalon et al. (2005); (13) Dai et al. (2000); (14) Maier et al. (2005); (15) Takabayashi et al. (2003); (16) Baums et al. (2005); (17) Brazeau et al. (2005); (18) Fukami et al. (2004).

the frequencies of introgressed alleles within populations of *A. cervicornis* due to factors such as limited dispersal, local inbreeding, and/or the differential selection against introgressed genes. Similar patterns of fine-scale genetic structure—often termed chaotic or genetic patchiness (Johnson and Black 1984; Hedgecock 1994)—have also been observed in a variety of other marine organisms (Johnson and Black 1984; Johnson et al. 1993; Hedgecock 1994; Li and Hedgecock 1998; Lenfant and Planes 2002; Pujolar et al. 2006) and are thought to result from local differences in selection (Johnson and Black 1984) and/or sweepstakes effects in reproduction or recruitment (Hedgecock 1994). More extensive sampling is needed to determine the extent of fine-scale genetic structure in *A. cervicornis* and elucidate the forces generating these highly localized introgression signatures.

Restricted Gene Flow in Reef Corals

A survey of coral population genetic studies (summarized in Table 4) reveals accumulating evidence for restricted gene flow in reef corals over large spatial scales (ca. 500–1200+ km). All 4 Caribbean studies indicate that restricted gene flow over 500 km is common. In the Indo-Pacific, where most studies have been conducted, significant but variable degrees of genetic structure have been detected in 11 out of the 15 coral species surveyed, and 2 additional species show significant population structure over 2000 km. Estimated population genetic structure in Indo-Pacific corals is typically lower than in Caribbean corals, suggesting that realized gene flow may be higher in Indo-Pacific corals. For example, allozyme data from the Great Barrier Reef (GBR) showed low to moderate population structure (F_{st} = 0.15) over spatial scales of 500–1200 km (Ayre and Hughes 2000, 2004). Higher genetic structure (F_{st} = 0.10–0.40) observed in the same corals between the GBR and Lord Howe Island 700 km away (Ayre and Hughes 2004) indicates that the absence of suitable reef habitats between distant locations can greatly limit gene flow. The Indo-Pacific data also show that genetic structure can vary substantially among geographic locations in the same species. For example, 3 allozyme studies of *Pocillopora*

damicornis detected varying genetic structure (F_{st} = 0.01–0.39) over similar spatial scales, approximately 400–650 km (Stoddart 1984; Adjeroud and Tsuchiya 1999; Ayre and Hughes 2000). Thus, results from one location clearly cannot be extrapolated to different regions. This argues for large-scale genetic surveys of Indo-Pacific corals across their entire ranges, which have not yet been completed.

Our study with *A. cervicornis* and the recent study by Baums et al. (2005) on *A. palmata* represent the first large-scale population genetic analyses of Caribbean corals. The microsatellite data of Baums et al. (2005) indicate that *A. palmata* 1) exhibits significant population structure across the wider Caribbean (F_{st} = 0.036, R_{st} = 0.153), 2) has been historically subdivided into 2 regional subpopulations, the Western Caribbean and Eastern Caribbean, with admixture in Puerto Rico, and 3) populations are mostly self-recruiting. Although direct comparisons of microsatellite and DNA sequence data are difficult, high levels of genetic structure observed for *A. palmata* (R_{st} = 0.153) and for *A. cervicornis* (Φ_{st} = 0.238) are comparable and demonstrate restricted gene flow in both Caribbean *Acropora* species. Our data are consistent with the West-East Caribbean population subdivision in *A. palmata* (e.g., Curacao in the East is highly distinct), but further East Caribbean sampling of *A. cervicornis* is needed to confirm this pattern. In addition to the Caribbean *Acropora*, recent genetic work with the 3 *Montastraea* species show similarly high levels of population structure (Φ_{st} = 0.20–0.22) between Panama and the Bahamas (Fukami et al. 2004). Thus, restricted gene flow seems to be common in the 2 main groups of Caribbean reef corals.

Gene Flow across the Wider Caribbean

Generalizations about patterns of gene flow in Caribbean reef organisms are difficult. Recent work with the goby *Elacatinus evelynae* (Taylor and Hellberg 2003) and reef coral *A. palmata* (Baums et al. 2005) have renewed interest in the possibility that the Caribbean has been historically subdivided into 2 regions—the Eastern and Western Caribbean—similar to previously proposed biogeographic provinces (Robins 1971; Briggs 1974). However, most Caribbean organisms do not show distinct genetic breaks. Instead, varying degrees of genetic structure have been detected in reef fish (Shulman and Bermingham 1995; Taylor and Hellberg 2003; Bowen et al. 2006), soft-corals in the Bahamas (Gutierrez-Rodriguez and Lasker 2004), and sponge-dwelling shrimps (Duffy 1993), whereas little to no population structure has been detected in a variety of other taxa including conch (Mitton et al. 1989), lobsters (Silberman et al. 1994), sea urchins (Lessios et al. 1999, 2001, 2003), and the majority of reef fish (Shulman and Bermingham 1995; Rocha et al. 2002). Most of these taxa have higher larval dispersal potentials (ca. 20+ days) than is likely for *A. cervicornis* (ca. 4 days, Vollmer SV, Fogarty N, unpublished data). Generally, the Caribbean genetic results demonstrate that planktonic duration is not always a good predictor for realized gene flow (Jones et al. 1999; Swearer et al. 1999; Barber et al. 2000; Cowen et al. 2000; Bowen et al. 2006). Because the genetic evidence for the 3 major Caribbean reef corals indicates that gene flow is limited among reefs over a minimum scale of 500 km, patterns of genetic connectivity in the reef corals themselves may serve as the best guide for setting the scale of conservation and management strategies on Caribbean reefs.

Conservation Implications for Caribbean Staghorn Corals

Restricted gene flow in *A. cervicornis* has important conservation implications for the species. Most populations of *A. cervicornis* have not recovered from the Caribbean-wide declines of past decades (Jaap et al. 1988; Aronson and Precht 2001; Precht et al. 2002), many populations are critically small (Miller et al. 2002; Precht et al. 2002), and newly settled *A. cervicornis* sexual recruits continue to be rare (Vargas-Angel et al. 2003). Regional differences in *A. cervicornis* indicate that populations separated by more than 500 km require their own conservation and management plans. The occurrence of introgression hot spots in multiple regions (albeit rare) show that gene flow can be low over spatial scales as small as 2 km. As a result, the recovery of *A. cervicornis* will be derived predominantly from local source populations and by not larval dispersal from distant reefs. Thus, it is imperative to protect the surviving populations of *A. cervicornis* through both local and regional conservation strategies, so that they will seed their own recovery.

Fortunately, our results do show that the numbers of unique genetic individuals (i.e., genets) of *A. cervicornis* on reefs today (58%) are comparable to pre-die off estimates (Neigel and Avise 1983). Thus, even small populations of *A. cervicornis* possess a reservoir of genetic variation (i.e., multiple genotypes) to successfully out-cross during sexual reproduction (Table 1). Local conservation of *A. cervicornis* has the potential to allow existing populations to recover locally via asexual fragmentation and, in the long term, allow the species to recolonize former habitat through sexual recruitment.

Conclusion

Population genetic data from corals are increasingly revealing the scales over which reef coral communities are likely to be interconnected by ecologically relevant levels of gene flow. In addition to the findings presented here, recent studies of the major reef-building coral from the Caribbean and Indo-Pacific (Table 4) indicate that dispersal in a diversity of reef-building coral species is limited over large spatial scales. Given that restricted gene flow over hundreds to thousands of kilometers may be true for many corals from diverse ecological settings, then long-distance larval dispersal from far-flung reefs cannot be relied on as a practical conservation tool to manage the health and recovery of coral reefs. In highly impacted coral communities like the Caribbean staghorn corals, protecting local source populations as seed banks to fuel future recovery is imperative, but they must be in close proximity to be effective.

Appendix 1. Geographic distribution of haplotypes for each gene by region and by population. Haplotypes are coded by a gene abbreviation and whether or not it was native (n) or introgressed (i) as in figure 2. White = native; gray = introgressed

	Panama						Florida		Bahamas				Caicos			Puerto Rico				Curacao			
Locus/ alleles	San Blas	Salt Creek	Crawl Cay	Casa Blanca	Belize	Yucatan	Florida Keys	Ft. Lauderdale	North San Salvador	Southwest San Salvador	Lee Stocking	Andros	*Montastrea* Reef	Patch Reef	Jamaica	San Juan	San Cristobal	Media Luna	Guanica	Jan Thiel	Fuik	Spaanse Water	Total
MtDNA																							
Mt_n1	1	1							1	1		1	4	1									10
Mt_n2										1			1			1		1	1	2	2	2	11
Mt_n3												1											1
Mt_n4														1			4			1	2	1	9
Mt_n5		2				1	1	1															5
Mt_n6					1	2																	3
Mt_n7					1																		1
Mt_n8					2																		2
Mt_n9					3																		3
Mt_n10														1	1								2
Mt_n11	1	3			4				4	5	1	1	8	2	1	2	4	2	2				40
Mt_n12																		2					2
Mt_n13												1	1							1			3
Mt_n14			2		1								1										4
Mt_n15													4										4
Mt_i1										1													1
Mt_i2	3	3	6	3				1	2	3	4		1	1	2				1	1		3	34
Mt_i3												1											1
Mt_i4														1									1
Mt_i5																	1		1				2
Mt_i6												2											2
Mt_i7											1												1
Mt_i8																	1						1
Mt_i9										1													1
Mt_i10							1						1	2							1		5
Mt_i11							1			1						1	1	1		1	2		8
Mt_i12														1									1
Total	5	9	8	3	12	3	3	2	7	13	6	7	21	10	4	4	11	6	5	6	7	6	158
MiniCollagen																							
MC_n1		7	4	1					6	4	3	5	15	3						1			49
MC_n2	8	7	6	5		5			6	8	7	3	23	9	4	8	12	12	8	9	12	6	158
MC_n3						1																	1
Total	8	14	10	6	0	6	0	0	12	12	10	8	38	12	4	8	12	12	8	10	12	6	208
CalM																							
Cal_n1	5	13	12	4		4	4	4	5	18	9	8	21	15	7	7	19	11	6	8	11	10	201
Cal_n2													2										2
Cal_i1	5	3	4	2		2	2		9	8	3	6	13	7	1	1	3	1	4	4	3	2	83
Total	10	16	16	6	0	6	6	4	14	26	12	14	36	22	8	8	22	12	10	12	14	12	286
*Pax*C																							
*Pax*_n1	4	11	10	5		5	4	3	6	21	7	11	39	17	6	8	19	2	8	9	10	9	214
*Pax*_i1	6	7	6	1		1		1	5	1	3	2	5	5			1	6	2	3	4	3	62
*Pax*_i2											2						2						4
*Pax*_i3									1	4		1											6
Total	10	18	16	6	0	6	4	4	12	26	12	14	44	22	6	8	22	8	10	12	14	12	286

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