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RESEARCH ARTICLE

Contrasting population genetic structures of sympatric, mass-spawning Caribbean corals

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Abstract Coral reef conservation management policy often focuses on larval retention and recruitment of marine fish with scant data available on important, less motile reef-building species such as corals. To evaluate the concept of population connectivity in corals, we tested whether broadcast spawning reproduction per se confers the same degree of dispersal to two sister species, *Montastraea annularis* (Anthozoa: Scleractinia; Ellis and Solander 1786) and *M. faveolata* (Ellis and Solander 1786), both dominant taxa in reefs of the northern Caribbean. Genetic analyses of ten nuclear DNA loci (seven microsatellite and three single-copy RFLP) reveal strikingly different patterns of population genetic subdivision for these closely related, sympatric species, in spite of likely identical dispersal abilities. Strong population genetic structure typified the architecture of *M. annularis*, whereas *M. faveolata* populations were principally genetically well mixed. A higher level of clonality was observed in *M. annularis* potentially because of a susceptibility to physical fragmentation. Clonality did not, however, significantly contribute to population genetic structure or low-level Hardy–Weinberg and linkage disequilibria observed in some populations. The lack of consistent association between reproductive mode and dispersal reinforces the perspective that population connectivity is not so much a function of predictable marine population source and sink relationships as is due to a more complex interface of oceanic currents interacting with and amplifying stochastic fluctuations in larval supply and settlement success. Our results support others promoting an overall ecosystem approach in marine protected area design.

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Introduction

Stony corals are the foundation of highly diverse marine ecosystems, providing structure, habitat, and primary productivity over vast areas of tropical near-shore habitat. Globally, many coral reef ecosystems are on a declining trajectory, as bleaching, disease, pollution, siltation from terrestrial run-off, fishing, and a variety of other natural and anthropogenic pressures, singly and in combination, take their toll (Gardner et al. 2003; Pandolfi et al. 2003; Bellwood et al. 2004; Jones et al. 2004). Degradation frequently is noted for Caribbean coral reefs (Hughes 1994; Hughes and Tanner 2000; Gardner et al. 2003) with a growing indication that the Great Barrier Reef system of

Australia also is deteriorating (Bellwood et al. 2004). A current focus of coral reef conservation is on estimating the degree of ecological interconnectivity of spatially disjunct reef systems (e.g., Bode et al. 2006; Cowen et al. 2006). Understanding the scale of dispersal for reef organisms will, in theory, provide a spatial context for drawing marine reserve boundaries as either protecting locally self-propagating populations or as encompassing larger-scale areas that rely on regionally separated larval pools. The actual degree of population connectivity in organisms capable of long distance dispersal, however, has been the subject of considerable debate (Roberts 1997; Jones et al. 1999; Swearer et al. 1999; Cowen et al. 2000, 2006; Rocha et al. 2002; Palumbi 2003; Taylor and Hellberg 2003). Levels of genetic subdivision indicative of local larval retention have been observed for a number of species with pelagic larvae, contradicting paradigms that pelagic larvae are effective long distance dispersers (Hamm and Burton 2000; Taylor and Hellberg 2003; Cowen et al. 2006).

Inferring degrees of connectivity may be particularly difficult for taxa within the reproductively-protean order Scleractinia because its members are known to outcross (Knowlton et al. 1997; Szmant et al. 1997), inbreed (Knowlton and Jackson 1993), hybridize (Knowlton et al. 1997; Szmant et al. 1997; Vollmer and Palumbi 2002) and propagate clonally (Veron 2000), all of which contribute in differing ways to population subdivision. Sedentary as adults, corals rely on free-floating larvae for dispersal and recruitment, and as expected, brooding species of coral, generally characterized as dispersal-challenged, have lower levels of gene flow than species with mass-spawning gametic phases (Hellberg 1994, 1996; Ayre and Hughes 2000). The degree to which corals with higher dispersal potentials are genetically structured, however, is not clear. When considering the population structure of only mass-spawning species, genetic mixing among reefs has been moderate to high and often if present, the resulting genetic subdivision is generally distance-dependent (Hellberg 1996; Ayre and Hughes 2000; Mackenzie et al. 2004). In other cases, however, even proximate sites within reefs exhibit genetic differentiation, particularly for highly clonal, broadcast-spawning species (Ayre and Hughes 2000). In the Caribbean basin, populations of *Acropora palmata* cluster into two major regions, one eastern and one western, between which no recent genetic interchange has occurred (Baums et al. 2005). Even patterns of population subdivision within a single mass-spawning species (*Plesiastrea versipora*) are not consistent, with highly restricted gene flow along the southeast Australian coast contrasting to genetic homogeneity over a similar range in the Ryukyu Archipelago of Japan (Rodriguez-Lanetty and Hoegh-Guldberg 2002). Clearly, no consensus view of dispersal and population subdivision in coral species has yet emerged.

Members of the *Montastraea annularis* species complex (Anthozoa: Scleractinia; *M. annularis* and *M. faveolata* [Ellis and Solander 1786] and *M. franksi* [Gregory 1895]) are generally slow growing and long-lived, and show low rates of sexual recruitment (Knowlton et al. 1997; Hughes and Tanner 2000). Ecologically, these boulder corals provide the structural reef integrity throughout much of the Caribbean and consequently are important conservation targets. As such, they are one of the most extensively studied reef-building corals in the western Atlantic (Knowlton et al. 1997; Szmant et al. 1997; Hughes and Tanner 2000; Budd and Pandolfi 2004; Fukami et al. 2004; Levitan et al. 2004). Reports that reef communities are shifting from these framework-building genera (e.g., *Montastraea* spp. and *Acropora* spp.) to non-framework building taxa (e.g., *Agaricia* spp. and *Porites* spp.) (Edmunds and Carpenter 2001; Knowlton 2001; Cho and Woodley 2002) make it particularly important that baseline genetic information for putatively declining species (such as *Montastraea* spp.) be garnered quickly. *Montastraea* spp. are hermaphroditic with gametes that are synchronously mass spawned annually in the late summer (Sammarco and Andrews 1988; Szmant 1991). Planulae larvae develop within 24 h of spawning and can remain at the surface for up to 96 h before settling (Wellington and Fitt 2003). Broadcast spawning and pelagic larva confer upon *Montastraea* spp. an expected ability to disperse widely. Previous studies in these corals have focused on their potential for hybridization because of their similar biology, overlapping spawning periods and the morphological diversity present among and within each of the species (Knowlton et al. 1992; Knowlton et al. 1997; Szmant et al. 1997; Fukami et al. 2004; Levitan et al. 2004). Although the three species, *M. annularis*, *M. faveolata* and *M. franksi*, exhibit similar spawning schedules over a 4–8 day period typically following the full moon in August, multiple isolating mechanisms appear to maintain the sympatry of these species (Levitan et al. 2004). For example, *M. franksi* begins spawning a day earlier than *M. annularis* and *M. faveolata*, and, if in a given day, all three are spawning, *M. franksi* precedes the other two species by at least 2 h. This temporal lead for *M. franksi* is particularly important with respect to its relationship with *M. annularis*, because laboratory-mating studies indicate a substantial degree of compatibility between gametes of these two species. *M. annularis* and

M. faveolata, on the other hand, spawn nearly synchronously, but fertilization trials have shown that their gametes are predominantly, but not completely, incompatible (Knowlton et al. 1997; Szmant et al. 1997; Levitan et al. 2004). Until the issue of hybridization in these corals formalizes, the species designations are at best tentative, but for our purposes, evaluating such closely related taxa with similar range distributions and mass-spawning reproductive strategies allows us to analyze the interdependence of dispersal potential and hydrodynamics on reef connectivity.

Here, we use a combination of ten polymorphic nuclear DNA markers constituted by three single-copy restriction-fragment-length polymorphisms (RFLP) and seven microsatellite, to test for associations between gene flow and reproductive strategy in populations of the dominant Caribbean coral reef species, *M. annularis* and *M. faveolata*. By including and comparing two marker types, we can minimize any marker-specific effects that could potentially distort an accurate picture of population connectivity. Although mitochondrial DNA often is used in population genetics studies of animals, it evolves much too slowly in coral to be useful at the population or even species levels (Shearer et al. 2002). Single-copy RFLP gene markers have predominantly been used in gene mapping and domestic animal and plant breeding studies (Paterson et al. 1988; Martin et al. 1989). These markers, however, also have proven effective in population genetics of natural populations for sorting out anomalies or uncovering hidden molecular variation not detected by other means (Karl and Avise 1992; Karl et al. 1992; Cattell and Karl 2004). Microsatellites are the current favorite tool of population biologists and as highly polymorphic loci are particularly useful for genotyping reproductively complex organisms such as corals because unique genets usually can be identified with a high degree of accuracy and precision. As one facet of a multidisciplinary and comprehensive evaluation of the state of Caribbean coral reefs, this genetic component can aid management authorities in matters concerning connectivity, heritable bleaching susceptibility, and transplantation strategies geared to maximize genetic diversity, and to maintain genetically distinct populations.

Materials and methods

DNA markers

Seven microsatellite and three anonymous single-copy nuclear DNA markers were isolated as described previously (Severance et al. 2004a, b). For the single-copy locus analyses, RFLP of polymerase chain reaction (PCR) amplification products were used to genotype individuals. In this di-allelic system, individuals were scored as either homozygous for the presence of, homozygous for the absence of, or heterozygous for cleavage at an endonuclease recognition site. Microsatellite genotypes were determined by the size of fluorescently labeled PCR fragments that were size sorted on an ABI 377 automated sequencer (Iowa State University Sequencing Facility). PCR conditions for amplifying field samples using both sets of markers were reported previously (Severance et al. 2004a, b).

Field samples

Using SCUBA, a total of 127 *M. annularis* and 152 *M. faveolata* samples were collected in water at depths from 0 to 25 m at four locations in the Western Atlantic (Table 1; Fig. 1). Unlike with fast-growing branching corals, collecting samples from the massive boulder-like corals is more threatening to the health of the coral; consequently utmost care was taken to minimize damage to sampled colonies. The number of samples collected at any one location was highly restricted by the governing marine authorities and by the number of colonies present at any given site. With respect to the latter, we collected fewer *M. annularis* individuals simply because they were less abundant at some sites and completely absent at others. Approximately 2–4 cm^2 sections of *M. annularis* and *M. faveolata* were removed with a hammer and chisel from the basal portion of the colony and placed in labeled plastic zip-lock bags. Samples were stored on ice immediately following the dive and placed in 90% ethanol for longer term storage as soon as feasible. Multiple sites separated by less than 10 km were sampled within each geographic location. At all sites, only one sample per coral head was collected and to the extent possible, only nonadjacent coral heads were collected to minimize multiple recording of the same individuals or clone mates. Likewise, our sampling methods specifically targeted colonies that were morphologically unambiguously either *M. annularis* or *M. faveolata*. Consequently, any colony of questionable taxonomic identity was avoided and the potential of collecting hybrids (Szmant et al. 1997) was minimized. Details concerning collection sites including the reefs sampled, depth, longitude and latitude coordinates, and the number of samples taken from each location are summarized in Table 1.

DNA extraction

DNA was extracted using a modified Chelex protocol (Walsh et al. 1991). Colony fragments of approximately 4 mm^2 were placed in 500 μL of 5% Chelex and boiled for 15 min. Samples were vortexed for 15 s and centrifuged for 5 min at 15,000 rpm. The supernatant was removed, placed in a new tube and extracted three times with 25:24:1 phenol:chloroform:isoamyl alcohol and once with 24:1 chloroform:isoamyl alcohol. The solution was incubated for 1 h at 65°C and then overnight at room temperature with a 4 M lithium chloride solution. The mixture was centrifuged for 30 min and the pellet resuspended in 50 μL of 1x TE (10 mM Tris–HCl, pH 7.5, 5 mM EDTA). Maintaining the stability of the DNA isolated in this way proved challenging; therefore, amplifications were performed as soon as possible after DNA isolation.

Population genetic analyses

Tests for conformance to Hardy–Weinberg genotype frequency equilibrium (HWE) expectations and for significant deviations from linkage equilibrium were performed using ARLEQUIN v. 2.00 (Schneider et al. 2000). Population sample pairwise F_{ST} estimates for single-copy RFLP data and significance tests also were performed using ARLEQUIN v. 2.00. F_{ST} values were estimated based on a count of the number of each allele (Weir and Cockerham 1984; Michalakis and Excoffier 1996; Schneider et al. 2000) and significance levels estimated by permuting genotypes between populations for 3,024 iterations and the probability (P) reflecting the proportion of permutations leading to an F_{ST} value equal to or larger than the observed. For microsatellite loci, sample pairwise *Rho* values, an unbiased estimator of Slatkin's R_{ST} (Slatkin 1995), and

Table 1 Details of sample collection location and sites and numbers of individuals collected at each site

Collection location and site	Depth (m)	Coordinates	Number of samples	
			M. annularis	*M. faveolata*
La Parguera Reef, Puerto Rico				
Beril Reef (PR1)	20	17°55′N 67°56′W	4	5
San Cristobal Reef (PR2)	0–5	17°54′N 67°04′W	12	10
Media Luna Reef (PR3)	1–20	17°56′N 67°03′W	14	15
		Total	30	30
Tulum Region, Yucatan, Mexico				
Patch Reef (YC1a)	7–14	20°02′N 87°28′W	12	15
Spur and Groove Reef 1 (YC1b)	7–14	20°02′N 87°28′W	19	26
Spur and Groove Reef 2 (YC2)	0–3	18°53′N 87°38′W	7	7
		Total	38	48
Lower Florida Keys, Florida, USA				
West Washerwoman Reef 1 (LK1)	15–25	24°33′N 81°34′W	12	23
West Washerwoman Reef 2 (LK2)	15–25	24°32′N 81°37′W	15	19
		Total	27	42
Dry Tortugas, Florida, USA				
Fort Shoals Reef (DT1)	10–15	24°37′N 82°52′W	26	20
Little Africa Reef (DT2)	0–3	24°38′N 82°55′W	6	0
NE Loggerhead Reef (DT3)	0–3	24°38′N 82°55′W	0	12
		Total	32	32
		Grand total	127	152

Sample site abbreviations used in the text are in parentheses

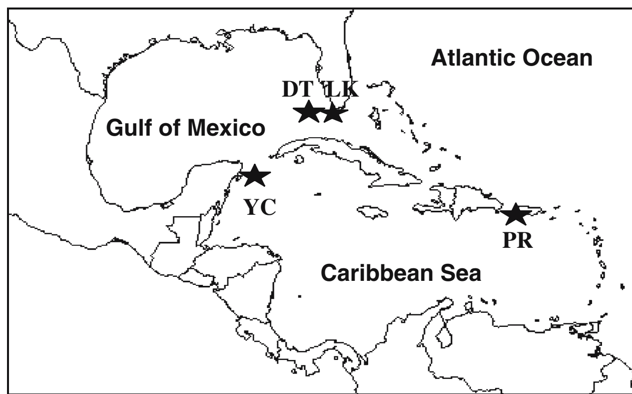

Fig. 1 Major geographic locations sampled in this study. Site abbreviations are as in Table 1

significance tests were calculated using RSTCALC version 2.2 (Goodman 1997). We chose *Rho* because there is an explicit consideration of mutation and microsatellite loci clearly do not evolve under the infinite allele model assumed with F_{ST}. Estimates of *Rho* were calculated across all loci and tested for significance based on 1,000 bootstraps, each with 1,000 permutations. All population genetic analyses were done separately for each set of molecular markers and with and without clonal replicates included (see text beyond). To minimize the possibility that null allele effects were contributing to the observed population genetic structure, analyses were also performed with and without the dinucleotide locus, MS2-17, which seemed to amplify some individuals less efficiently than the other markers. Sample sites within reefs were pooled if sample pairwise comparisons of F_{ST} and *Rho* values were not significantly different from zero. Isolation by distance was tested using a linear correlation coefficient of log transformed geographic distance versus Nei's D (Nei 1972), $\delta\mu^2$ (Goldstein et al. 1995), and chord distance (Cavalli-Sforza and Edwards 1967) which were calculated using the program MICROSAT (Minch 1995). Geographic distances were estimated as the most direct aquatic route between sites.

For each population, multi-locus genotypes, including microsatellite and single-copy loci, were sorted in Microsoft Excel and unique genotypes were identified. Evaluating clonality using microsatellite markers offers distinct advantages over other marker based systems because the high mutation rate at these loci generates a large number of alleles per locus (Sunnucks et al. 1996; Gomez and Carvalho 2000; Reusch et al. 2000). The microsatellites used here averaged approximately 21 alleles per locus (Severance et al. 2004a), indicating that they are likely to be highly sensitive in the identification of clonal genotypes. Nevertheless, we tested the probability that each identical genotype could be the result of sexual reproduction using MLGSIM (Stenberg et al. 2003). Corresponding critical *P* values were calculated using 10,000,000 simulations. Significant differences between species in the number of clonal genotypes relative to non-clonal genotypes were tested by chi-square analyses.

Results

Hardy–Weinberg equilibrium

For both species, significant deviations from HWE were present and all but one were heterozygote deficits. In *M. annularis*, 13 of the 44 locus-by-population tests (29.5%) deviated significantly before sequential Bonferroni correction. Seven of these were for the loci MS12 and MS2-17, which were two of the most diverse loci with 29 and 27 alleles, respectively, (Severance *et al.* 2004a). In *M. faveolata*, 9 of the 49 tests (18.4%) deviated significantly before sequential Bonferroni correction. Seven of these were for MS12 and MS2-17 where 24 and 29 alleles were seen in this species. No other locus showed consistent deviations across samples. The Dry Tortugas samples of both *M. annularis* and *M. faveolata* deviated at seven and three of the ten loci, respectively. This result persisted when clonal genotypes were removed and when sites within the Dry Tortugas were analyzed separately. No other sample had a preponderance of loci that deviated from HWE expectations. All significant differences remained so after sequential Bonferroni correction ($P = 0.01$) (Rice 1989).

Population genetic structure

Sample pairwise F_{ST} and *Rho* estimates between collection sites within locations were not statistically different from zero so they were pooled except for the Yucatan locations. Here, *M. annularis* individuals from the two YC1 sites (YC1a and YC1b) were indistinguishable but different from YC2, so we pooled the YC1 sites but not YC1 with YC2. Although the *M. faveolata* samples from these sites were not genetically statistically differentiated, they were kept separate to facilitate interspecific comparisons. The resulting microsatellite *Rho* and single-copy F_{ST} values for pairwise comparisons of major locations are shown in Tables 2 and 3. In *M. annularis*, significant inter-reef genetic subdivision was indicated for eight of the ten microsatellite and for seven of the ten single-copy pairwise location comparisons (Table 2). The average pairwise

population *Rho* was 0.11 ± 0.07 (SD) and $\bar{F}_{ST} = 0.38 \pm 0.29$. Conversely, for *M. faveolata* there was little to no significant among location differentiation with only one each of the ten pairwise *Rho* or F_{ST} values significantly different from zero (Table 3). The average *Rho* (0.01 ± 0.02) and $\bar{F}_{ST}(0.03 \pm 0.03)$ for *M. faveolata* also were significantly less than the values estimated for M. annularis ($P \leq 0.01$; 1-tailed *t* test; Sokal and Rohlf 1995). F_{ST} values of the single-copy markers were generally larger than the *Rho* values of the microsatellites, which was not surprising given the mutational mode differences between these two types of loci. Nevertheless, both sets of markers reflected the same pattern of interspecific differences (i.e., *M. annularis* was more genetically structured than *M. faveolata*), thus verifying that the observed structure is not a marker-specific phenomenon. Similarly, removal of the possible null-allele-associated locus MS2-17 from the analyses did not significantly change resulting *Rho* values in these comparisons. There was no significant association between genetic and geographic distance even for *M. annularis* where most pairwise tests of population differentiation were significant (data not shown).

It is possible that ascertainment bias from developing the markers with *M. annularis* may account for at least some of the difference seen between the species. We do not, however, believe that this is the case here. We have shown that these loci are highly polymorphic (Severance et al, 2004a, b) and that the degree of variability is nearly identical in both species (see supplemental material A and B). Further, if ascertainment bias existed, we would expect to see a higher heterozygosity and lower F_{ST} in the species from which the markers were developed (i.e., *M. annularis*) when, in fact, we observe just the opposite.

Clonality

Individuals that possessed an identical set of alleles (i.e., genotype) at all ten nuclear loci were considered clones. Most individuals appear to have been produced by sexual reproduction as evidenced by a preponderance of unique genotypes in the sample (Table 4). Identical multi-locus genotypes, however, were observed in all populations (except YC2) from both species. No sharing of identical genotypes occurred between populations in major geographic regions. By using the program MLGSIM (Stenberg et al. 2003), we estimated the probability that any of the observed putative clonal genotypes was actually the result of sexual reproduction was less than 10^{-15}. This probability was significant compared to the simulated critical values at $P \leq 0.05$. We conclude, therefore, that the

Table 2 Population pairwise genetic divergence estimates for *Montastraea annularis* individuals surveyed and the number of individuals screened (*N*; first number is for single copy and second number is for microsatellite loci)

	N	PR	YC1	YC2	LK	DT
PR	28/28	–	**0.08 (0.07)**	**0.19 (0.24)**	0.01 (0.01)	**0.10 (0.09)**
YC1	26/31	0.00 (0.00)	–	**0.11 (0.12)**	0.02 (0.02)	**0.12 (0.10)**
YC2	7/7	**0.74 (0.72)**	**0.70 (0.70)**	–	**0.14 (0.19)**	**0.23 (0.23)**
LK	27/27	0.04 (0.04)	0.00 (0.00)	**0.67 (0.66)**	–	**0.06 (0.05)**
DT	29/31	**0.48 (0.45)**	**0.40 (0.40)**	**0.47 (0.46)**	**0.33 (0.31)**	–

Below the diagonal are single-copy F_{ST} estimates and above are microsatellite *Rho* values. Numbers in parenthesis are *Rho* and F_{ST} values recalculated excluding clonemates (see text for details)

Values statistically different from zero ($P \leq 0.05$) are in bold

Table 3 Population pairwise genetic divergence estimates for *Montastraea faveolata* individuals surveyed and the number of individuals screened (*N*; first number is for single copy and second number is for microsatellite loci)

	N	PR	YC1	YC2	LK	DT
PR	28/29	–	0.02 (0.01)	0.00 (0.00)	0.01 (0.02)	**0.05** (0.04)
YC1	40/41	0.00 (0.00)	–	0.00 (0.00)	0.01 (0.03)	0.03 (0.03)
YC2	7/7	0.02 (0.01)	0.04 (0.04)	–	0.00 (0.01)	0.00 (0.00)
LK	31/42	0.03 (0.04)	0.01 (0.01)	**0.10 (0.10)**	–	0.01 (0.01)
DT	30/31	0.00 (0.01)	0.00 (0.00)	0.05 (0.05)	0.00 (0.00)	–

Below the diagonal are single-copy F_{ST} estimates and above are microsatellite *Rho* values. Numbers in parenthesis are *Rho* and F_{ST} values recalculated with clonal individuals excluded (see text for details)

Values statistically different from zero ($P \leq 0.05$) are in bold

Table 4 Clonality in *Montastraea* spp. observed in this study

	N	Genotypes			Individuals	
		Number of unique	Number of clonal	Clonal (%)	Number of clonal	Clonal (%)
M. annularis						
PR	28	25	3	12.0	6	21.4
YC1	31	29	2	7.0	4	12.9
YC2	7	7	0	0.0	0	0.0
LK	27	24	2	8.3	5	18.5
DT	31	26	3	11.5	8	25.8
Total	124	111	10	9.0	23	18.6
M. faveolata						
PR	30	29	1	3.5	2	6.7
YC1	41	39	2	5.1	4	9.8
YC2	7	7	0	0.0	0	0.0
LK	41	38	3	7.9	6	14.6
DT	33	32	1	3.1	2	6.1
Total	152	145	7	4.8	14	9.2

identical genotypes observed were generated via asexual reproduction.

Over all samples, the total percent of clonally produced individuals in *M. annularis* ($x = 18.6\%$) was significantly higher than that observed in *M. faveolata* ($x = 9.2\%$; $P \leq 0.025$; χ^2 test). The magnitude of asexual reproduction varied among populations (Table 4). For *M. annularis*, Puerto Rico and the Dry Tortugas had the highest percentage of clonal individuals (21.4 and 25.8%, respectively). In general, the *M. faveolata* populations had few clones, except for the LK sample where 14.6% of the sampled individuals were clonally derived (Table 4). Although clonality did not represent the predominant mode of reproduction among our populations, we felt compelled to reanalyze our genetic structures excluding clonemates, especially with respect to *M. annularis*, since this species was associated with both higher levels of genetic subdivision and clonality. The degree of significant population genetic subdivision remained unchanged following re-analysis (Tables 2, 3).

Linkage disequilibria

Nonrandom associations between loci revealed that significant associations of microsatellite alleles occurred in most populations of both species (data not shown). No locus pairs, however, consistently were linked, suggesting that the deviations are not due to physical linkage. For *M. faveolata*, none of the 15 possible single-copy dilocus comparisons and only 11 of the 105 (10.5%) possible microsatellite dilocus comparisons showed statistically significant linkage ($P \leq 0.01$). For *M. annularis*, zero of the 15 single copy and 33 of the 105 (31.4%) microsatellite dilocus comparisons were statistically significantly linked ($P \leq 0.01$). Two populations, the Dry Tortugas and the Lower Keys, accounted for 27 of the significant microsatellite disequilibria (16 and 11, respectively). These populations also indicated relatively higher frequencies of clonal reproduction. Surprisingly, Puerto Rico, despite a high frequency of clones, had only three di-locus comparisons, which were in disequilibrium. Reanalysis of linkage disequilibria with clonal individuals removed resulted in a decrease of the number of linked loci for the Lower Keys population from 11 to 7 but no change for the Dry Tortugas population. Reanalysis without pooling sample sites within regions did not change the number of linked loci.

Discussion

In our study, two sister species of mass-spawning Scleractinian coral exhibited very different population genetic structures, indicating that common reproductive mode need not imply common patterns of gene flow. Whereas sites within reefs were generally undifferentiated, populations of *M. annularis* among major geographic regions showed significant interpopulation genetic divergence. This is characteristic of a restriction in gene flow among the northern Caribbean populations examined in our analysis. To the contrary, *M. faveolata* populations were genetically indistinguishable throughout the same range in spite of nearly identical larval dispersal ability. These results demonstrate that realized dispersal, at least for *Montastraea* spp. cannot be accommodated under a single model of larval exchange. In reference to geography or larval strategy, the genetic patterns revealed here do not correspond to either a strictly open model of larval dispersal mediated by oceanic currents, or a closed model of restricted dispersal and local recruitment. Spawning strategy or putative larval dispersal ability simply are not reliable predictors of the potential for panmixia, and other ecological or evolutionary processes must underlie the discordant genetic patterns. It is conceivable that even if two species were identical in all important respects, as long as there is non-synchronized variance around mean life history parameters among species, confluence of this variance with environmental variance can result in a benefit to one species without necessarily benefiting the other. In other words, even in the absence of differences in larval biology, *M. faveolata* can have a good spawning and settlement year, whereas *M. annularis* does not. Given the rarity of sexual recruitment and the longevity of the species, the effect of any chance

differences is likely to persist for a long time. Collectively, this and other studies (e.g., Ayre and Hughes 2000, 2004; Miller and Ayre 2004) reinforce that coral population structure, like coral life-history, is complex and likely influenced by numerous factors including geographic scale and micro- and macro-physicalities specific to individual reefs.

The dominant mode of reproduction for *Montastraea* spp. is considered to be sexual (Szmant 1991), and therefore, the finding of clonality in both species in the present study is noteworthy. Clonality in these species contrasts with previous allozyme studies where all *M. annularis* and *M. faveolata* samples from Curaçao and Panama had unique genotypes (sample sizes were 25 and 43, respectively; Knowlton et al. 1992; Van Veghel and Bak 1993). The degree of clonality, therefore, is more likely a consequence of extrinsic influences rather than an inherent aspect of the organism's mode of reproduction. For example, asexual propagation via polyp expulsion during periods of unfavorable conditions has been reported in *Favia favus* in the Red Sea and *Oculina patagonia* in the Mediterranean Sea (Kramarsky-Winter et al. 1997). Given the declining population sizes and health of Caribbean corals (Gardner et al. 2003), this asexual survival strategy cannot be ruled out, although its occurrence in *Montastraea spp*. has not been documented. A more likely explanation and one that accounts for the differences observed between the species, however, may be physical colony fragmentation. The importance and association of clonality via colony fragmentation and disturbance has been well documented for coral (Tunnicliffe 1981; Hughes et al. 1992; Coffroth and Lasker 1998). Fragmentation and disturbance also may explain the differences in the apparent rates of clonality seen among the *Montastraea* morphotypes. Unlike the broad-based *M. faveolata*, the more columnar and sometimes top-heavy growth form of *M. annularis* is particularly predisposed to physical fragmentation (Edmunds 1994), and lobes could be broken off and scattered by storms. A similar growth form was believed to have enabled a now extinct organ-pipe *M. annularis*-like morphotype to colonize regions of high illumination in shallow water habitats, but predisposed it to fragmentation during times of disturbance (Pandolfi et al. 2002). Hurricanes can cause substantial damage to coral reefs, and because coral reefs in the Caribbean have been subjected to considerable storm activity over the past few decades (Rogers et al. 1991; Rogers 1992; Gardner et al. 2003), such disturbances likely are a proximate force for colony fragmentation in *M. annularis*. In addition, concerns about changes in ocean chemistry due to global warming resulting in carbon-dioxide-induced coral skeletal dissolution (Kleypas et al. 1999; Hughes et al. 2003) are particularly relevant to this species, as this predicted climate change would act to compound an already structurally compromised physical morphology of *M. annularis*.

During the initial colonization of these reefs, it is possible that they were settled by cohorts of larvae from geographically subdivided and genetically differentiated subpopulations resulting in admixture. Reefs would be similarly admixed if, over the course of the history of a reef, self-recruitment (i.e., larvae recruiting back to reefs from which they were spawned) was low and larval sources for particular locations frequently changed depending on hydrodynamic conditions (Wolanski 1994). Our observed deviations from Hardy–Weinberg genotypic frequency equilibrium and linkage equilibrium in some populations are consistent with mixing of genetically differentiated populations resulting in admixture (e.g., Dry Tortugas). We do not, however, see indications of widespread departures from equilibrium and therefore do not believe it is a dominant feature of underlying evolutionary processes occurring in these *Montastraea* species. Nevertheless, it is interesting that the population most affected by both Hardy–Weinberg and linkage disequilibria was the Dry Tortugas *M. annularis* population, even when the factors of clonality and null-allele effects were removed from the analyses. This location is considered to reside in an oceanographic hotspot (Lee et al. 1994; Lee and Williams 1999) that is particularly subjected to temporal micro- and meso-scale current fluctuations.

Large and small-scale oceanic water circulation patterns can interpose between random events and the biology of a species and may account for the contrasting patterns of genetic connectivity observed in this study. Water flow in the Caribbean basin is complex with current patterns characterized by the presence of eddies, meanders, and transient gyres that can act as mechanisms for larval access to and retention in inshore settlement sites (Yeung and McGowan 1991; Lee et al. 1992, 1994; Criales and Lee 1995; Lee and Williams 1999; Limouzy-Paris et al. 1997; Yeung and Lee 2002, Cowen et al. 2006). Figure 2 illustrates the complexity of surface current movement as tracked by 294 drift buoys released from 1978 to 2003 and archived and analyzed by the National Oceanographic and Atmospheric Administration, Atlantic Oceanographic and Meteorological Laboratory program (Gyory et al. 2005). This plot shows a considerable number of areas devoid of tracks as well as numerous eddies where buoys are temporarily entrained in local vortices (e.g., Fig. 2 bold track). Similarly, Murphy and

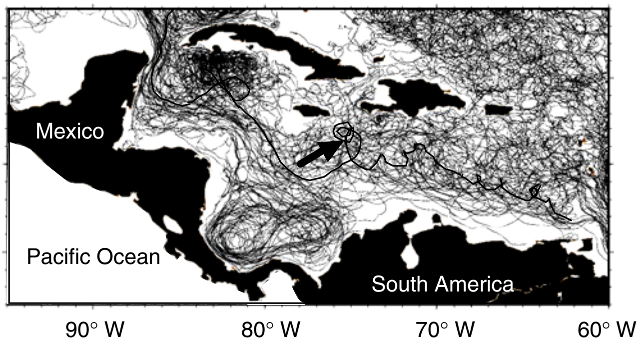

Fig. 2 Spaghetti plot tracks for 294 near-surface drift buoys from 1978 to June 2003. This figure is based on, and modified from, the National Oceanographic and Atmospheric Administration, Atlantic Oceanographic and Meteorological Laboratory Drifting Buoy Data Assembly Center data (see Gyory et al. 2005). All of the buoys were released in the southeastern Caribbean (i.e., lower right of the figure) and the principle direction of flow is to the northwest (i.e., upper left of the figure). The bold path corresponds to the track of buoy 09526392 from late March to early November 1996. During the August spawning season of *Montastraea* spp., the buoy spent the first three weeks in the loop indicated with an *arrow*

Hurlburt (1999) using linear and non-linear simulation models have demonstrated how decaying rings broken off from the North Brazil Current during retroflection are advected through the Lesser Antilles and form anticyclonic eddies. These eddies transit the Caribbean, often intensifying greatly along the way, before emerging into the Gulf of Mexico through the Yucatan Channel approximately 10 months after entering the basin. Larvae entrained in these eddies would only be able to settle if or when these cohesive water masses next encounter suitable habitat. A linear relationship of geographic distance between reefs and degree of genetic connectivity, therefore, would not be expected. With our data, correlations of genetic [$(\delta\mu)^2$ and Nei's D] with geographic distances were not significant (data not shown) for either *M. annularis* where most pairwise tests of population differentiation were significant or for *M. faveolata* where genetic homogeneity indicative of widespread dispersal would presumably reflect isolation-by-distance mechanisms. Given a somewhat limited geographical sampling, however, we may lack the power to detect isolation-by-distance, if present.

With respect to our genetic data in the context of ongoing oceanographic research in this locale (Yeung and McGowan 1991; Lee et al. 1992, 1994; Criales and Lee 1995; Lee and Williams 1999; Limouzy-Paris et al. 1997; Yeung and Lee 2002), we posit that genetic connectivity among reefs due to ocean currents will be significantly influenced by factors peculiar to each species, spawning season, spawning year, and geographical location as well as inherent biological factors. The heterozygote deficiencies of the Dry Tortugas, for example, could very well be the result of localized eddies resulting in enhanced settlement of related recruits in this region for *M. annularis* but not for *M. faveolata*. The lack of divergence among *M. faveolata* populations or the presence of divergence among *M. annularis* may simply be a result of chance timing of larval entrainment in eddies either enhancing or retarding inter-reef dispersal. Since these are long-lived organisms as adults (a typical one-meter diameter, adult colony is at least a century old [Hughes and Tanner 2000]), the genetic signal of historical events also will be detected far into the future. Taken together, we believe that the highly variable and sometimes counterintuitive inferences drawn from studies of population connectivity in corals, Caribbean and Pacific alike, are a reflection of the variable hydrodynamic regime in which the species live.

The inability of species to realize a level of population connectivity commensurate with intrinsic dispersal potential can be attributed to a complex web of interactions (Hedgecock 1986; Connell et al. 1997). The population genetics of these two *Montastraea* spp. indicate that connectivity must be gauged on a species by species basis even for sympatric, closely related taxa with seemingly identical life history characteristics. This conclusion holds important implications for the conservation and management of natural marine systems. The establishment of marine reserves as a fisheries management and conservation tool is fast replacing classical, target-species catch and effort quota approaches, but debate centers on the placement, size, and arrangement of marine protected areas (MPAs) (Ogden 1997; Roberts and Schmidt 1997). In theory, MPA design and management strategies preserve processes acting at ecological scales (i.e., dispersal and recruitment among present-day populations); yet genetically defined connectivity encompasses evolutionary scales (Leis 2002). The results of this research emphasize that indirect assessments based solely on presumed dispersal potential or even population genetic structure may be misleading. Considerations such as the frequency of clonal reproduction or temporal variation in reproductive success may be more important than larval dispersal potential in defining the health or connectivity of coral reefs. As such, the results add additional support for the need for a total ecosystem approach to the design of marine protected areas. Accurately defining distinct species groups or habitats as open (Roberts 1997) or closed (Cowen et al. 2000) may be impossible at anything but the species level. Delineating marine reserves, therefore, may be as data intensive as traditional single-species catch quotas.

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