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Students: ZEBULON MARTIN, Otterbein University, JAMES BUSCH, Washington & Lee University, SHANNON DILLON, Colgate University, SARAH HOLMES, Beloit College, GABRIELA GARCIA, Oberlin College, SARAH BENDER, The College of Wooster, ERIN PEELING, Pennsylvania State University, GREGORY MAK, Trinity University, THOMAS HEROLD, The College of Wooster, ADELE IRWIN, Washington & Lee University, ILLIAN DECORTE, Macalester College

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Research Advisor: Karl R. Wirth, Macalester College

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INVESTIGATIONS OF RESILIENT ACROPORA COMMUNITIES IN BELIZE: RELATIVE AGING AND INTRASPECIFIC DIVERSITY CALCULATIONS OF SPECIES USING MICROSATELLITE MARKERS AND SOMATIC MUTATIONS

ADELE IRWIN, Washington and Lee University
Research Advisor: Lisa Greer

INTRODUCTION

Coral reefs world-wide are in serious decline in response to rising global temperature, overfishing, rising sea level, disease, sedimentation, and ocean acidification. *Acropora*, historically one of the most crucial genera of coral due to its superior volume and mass, has experienced 98% decline in the Caribbean in just a few decades in response to increasing environmental stress (Bowden-Kerby et al. 2011; Ginsburg 1956; Knowlton 1992). Select *Acropora cervicornis* and *palmata*-dominated sites have been reported in Honduras (Keck et al. 2005), the Dominican Republic (Lirman et al. 2010), Mexico (Larson et al. 2014), Florida (Vargas-Angel et al. 2003), and Belize (Peckol et al. 2003; Brown-Saracino et al. 2007; Macintyre & Toscano 2007) where *Acropora spp.* thrive in anomalous conditions of high live abundance. Additionally, sites including Florida (FWRI & DTNP 2010), Curacao, Lesser Antilles (Japaud et al. 2014), and Belize (Fogarty 2010; Fogarty et al. 2012; Richards & Hobbs 2015) have also been reported where the hybrid *Acropora* species of *A. cervicornis* and *A. palmata*, *A. prolifera*, has reached relatively high abundances and more frequent occurrences despite its infrequent documentation in the past (Goreau et al. 1959; Lang et al. 1998; Cortes 2003; Willis et al. 2006).

Analysis of genotypic diversity and clonal age have not been conducted at these sites of reported high *Acropora* abundance, and may provide insight into the organization of these thriving reefs. Genotypic

diversity data facilitates analysis of a population's sexual recruitment and future fitness in the face of adverse conditions (Zubillaga et al. 2008; Downing et al. 2012; Altizer et al. 2003; Reed and Frankham 2003; Reusch et al. 2005). Some *Acropora* studies suggest that the reported high abundance indicates high potential for sexual recruitment (Vargas-Angel et al. 2003; Zubillaga et al. 2008; Lirman et al. 2010; Larson et al. 2014), but this has not been confirmed. Clonal age, or time since a clone's sexual propagation, facilitates analysis of clonal persistence or newness. (Ally et al. 2008; Weiher et al. 1999; Witte et al. 2010; Eriksson et al. 2000). Clonal age data may also provide clarification for the history of *A. prolifera*'s spread and emergence, a topic currently debated due to the hybrid's lack of fossil record (Budd et al. 1994) and absence from published visual site surveys.

Genotypic diversity and clonal age data can be collected from microsatellite DNA from live coral tissue. Calculating clonal age in corals has proved difficult due to lack of feasible methods for recording their histories. Methods have been used to date clonal species such as *Populus tremuloides* (trembling aspen) by considering the number of somatic mutations seen in microsatellite DNA samples, colony growth rates, and somatic mutation rates (Ally et al. 2008). Our collaborator Meghann Durante (Pennsylvania State University) applies this somatic aging method (in prep) to coral populations to calculate minimum and maximum age estimates of clones. It is appropriate to apply this somatic aging method to coral clones because corals transmit their somatic mutations to

fragment (Orive et al. 2001; Schweinsberg et al. 2014) and propagule (Shikina et al. 2012) offspring.

We report three sites with exceptional *A. cervicornis*, *A. palmata*, and *A. prolifera* abundance offshore of Ambergris Caye, Belize; Coral Gardens, Manatee Channel, and Rocky Point (Figure 1, Greer et al., this volume); and use five microsatellite markers to analyze genotypic diversity and clonal ages of these *Acropora* populations. This study aims to determine the clonal structure and predict the level of sexual recruitment at these sites, and to apply Durante's method to calculate somatic ages of coral clones for the first time.

METHODS

Sampling

1 cm³ samples were collecting from live branch tips using bone cutters, stored in 95% ethanol, and refrigerated until DNA extractions. In 2013 at Coral Gardens *A. cervicornis* was sampled hap hazardously (n=60). In addition, all encountered colonies of *A. palmata* (N=78) and *A. prolifera* (N=48) were sampled. Additional sampling in 2014 was designed to increase likelihood of sampling clones. At Coral Gardens *A. cervicornis* (n=158) samples were taken by creating 5 m circle plots in which a center point was created and in 4 different directions a sample was collected every 5 m, with no plots overlapping. At Manatee Channel *A. prolifera* samples (n=78) were collected using the same circle plot method, and every observed individual colony of *A. cervicornis* (N=20) and *A. palmata* (N=15) were sampled. At Rocky Point *A. prolifera* was sampled hap hazardously (n=32) due to irregular patch shape.

Genotyping and diversity calculations

Tissue DNA was extracted and amplified using the methods described in Baums et al. (2005). Five microsatellite loci (Baums 2005) were used to distinguish genets. Intraspecific genotypic diversity (Go/Ge), evenness (Go/Ng), and richness (Ng/N) were calculated within study sites and combined study sites (Belize) using the methods described in Baums et al. (2006). Data was compared against aggregate data from Baums et al. (2006) to make relative inferences.

Somatic mutations

Once genets were identified, somatic mutations of individual ramets were distinguished (Durante, in prep). Next we established the datable samples by distinguishing clones with at least five ramets. Genetic distance of each of these clonal groups containing at least one mutated individual was calculated using Genalex functions Euclidian distance and π divergence. The genetic distance and the mutation rates established by Durante (lowest=1.43E-05, highest=1.07E-04) were then applied to the equation described in Ally (2008) to obtain the maximum and minimum ages of each clone. Mutation rates were developed by comparing published *A. palmata* growth rates to numbers of somatic mutations of collected samples and the size of the colony they were collected from.

RESULTS

Genotypic diversity

All *Acropora* populations at all study sites and also when observed together collectively as a "Belize" population had genotypic characteristics (diversity, Go/Ge; evenness, Go/Ng) classifying them somewhere between Baums et al. (2006) groups "asexual" (Go/Ge=0.05, Go/Ng=1) and "mostly asexual" (Go/Ge=0.15625, Go/Ng=0.3875) (Table 2). *A. prolifera* at Manatee Channel was the only population to show complete clonality and thus asexuality ($G_e/G_c=0.014$, $G_o/N_g=1$). The samples of *A. prolifera* at Coral Gardens and *A. cervicornis* and *A. palmata* at Manatee Channel represent complete censuses of the populations present. Number of unique clones (N_g) of *A. cervicornis* were 10 (CG) and 8 (MC); of *A. palmata* 23 (CG) and 8 (MC); of *A. prolifera* 9 (CG), 1 (MC), and 4 (RP) (Fig. 1, Table 1). *A. cervicornis* and *A. palmata* were not present at Rocky Point.

Somatic Ages

From our 328 *Acropora* samples, we were able to calculate minimum and maximum age estimates for 19 of the 63 clonal populations because 5 or more ramets were collected (Fig. 2, Table 2). Coral Gardens showed a wide range of clonal ages across all *Acropora* populations. Coral Gardens *A. cervicornis*

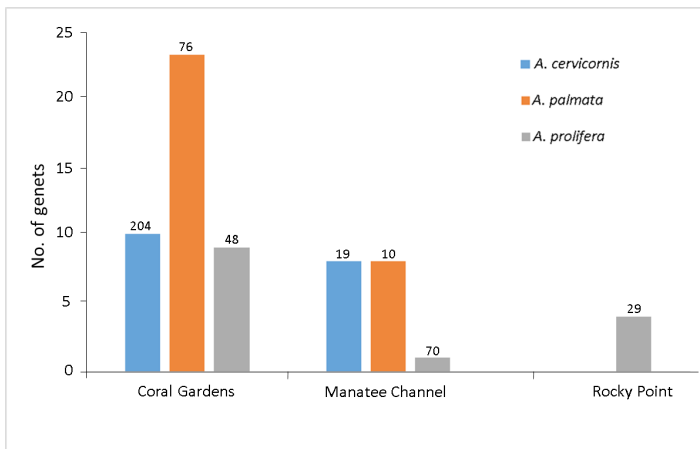


Figure 1. Clonal composition of *A. cervicornis*, *A. palmata*, and *A. prolifera* samples collected across study sites, expressed in number of genets (clones) found. Sample sizes are indicated above each bar.

community had 2 new clones (0-62 years), 2 clones 62-460, 1 clone 179-1337, 1 clone 393-2931, and 1 clone 409-3052. The *A. palmata* community had 1 new clone (0-62), 1 clone 187-1397, 1 clone 219-1636, and 1 clone 461-4191. The *A. prolifera* community had 2 new clones (0-62) and 1 clone 281-2096. Manatee Channel showed all new clones (0-62), with 1 clone aged from each *Acropora* population. Rocky Point showed a combination of new and old of *A. prolifera* clones, 1 new clone (0-62) and 1 clone 156-1164.

DISCUSSION

Acropora populations across all study sites show a range of asexual to mostly asexual reproductive behavior. This asexual to mostly asexual reproductive behavior is also seen when considering populations together as a Belize population. This overall trend indicates that fragmentation is the predominant mode of reproduction in this region, and that not much local recruitment is taking place to increase

Site	Species	N	Ng	Ng/N	Go	Go/Ge	Go/Ng
Coral Gardens	<i>A. cervicornis</i>	204	10	0.049	0.731	0.004	0.073
	<i>A. palmata</i>	76	23	0.303	0.821	0.011	0.036
	<i>A. prolifera</i>	48	9	0.188	0.857	0.018	0.095
Manatee Channel	<i>A. cervicornis</i>	19	8	0.421	0.781	0.041	0.098
	<i>A. palmata</i>	10	8	0.8	0.807	0.081	0.101
	<i>A. prolifera</i>	70	1	0.014	1	0.014	1
Rocky Point	<i>A. prolifera</i>	29	4	0.138	0.9	0.031	0.225
Belize	<i>A. cervicornis</i>	223	18	0.081	0.749	0.004	0.042
	<i>A. palmata</i>	86	31	0.361	0.815	0.01	0.026
	<i>A. prolifera</i>	147	14	0.095	0.871	0.006	0.062

Baums et al. 2006 Sexuality Groups' Averages

Group	<i>A. palmata</i>	N	Ng	Ng/N	Go	Go/Ge	Go/Ng
1, asexual		20	1	0.05	1	0.05	1
2, mostly asexual		22.625	9.125	0.4025	3.5125	0.15625	0.3875
3, mostly sexual		21.75	13.75	0.63625	9.77375	0.4525	0.69625
4, sexual		17.5	17	0.975	16.59	0.955	0.98

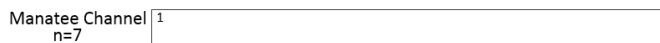
Table 1. Characteristics of genotypic diversity of samples from three study sites (top) and Belize (combined data from the study sites, middle). Below the double bars is data collected from Baums et al. 2006, describing the averages of data from four groups they characterized as asexual, mostly asexual, mostly sexual, and sexual; included for comparison. They classified groups with combined Ng/N and Go/Ge values. Key to abbreviations: N, number of colonies sampled; Ng, number of unique genets; Ng/N, genotypic richness; Go, observed genotypic diversity; Go/Ge, genotypic diversity (Ge=expected genotypic diversity); Go/Ng, genotypic evenness.

Reef	Species	Clonal ID	Transect	N	π	Min. age	Max. age
Coral Gardens	<i>A. cervicornis</i>	4	3	37	NA	0	62
	<i>A. cervicornis</i>	5	2	7	NA	0	62
	<i>A. cervicornis</i>	10	T1	19	0.0263	62	460
	<i>A. cervicornis</i>	11	T1	19	0.0263	62	460
	<i>A. cervicornis</i>	13	T4	37	0.0766	179	1337
	<i>A. cervicornis</i>	17	T5	30	0.1678	393	2931
	<i>A. cervicornis</i>	18	T2	43	0.1748	409	3052
	<i>A. palmata</i>	6	5	5	NA	0	62
	<i>A. palmata</i>	14	T3	5	0.08	187	1397
	<i>A. palmata</i>	15	T3 & T4	20	0.0937	219	1636
	<i>A. palmata</i>	19	T1	6	0.24	561	4191
	<i>A. prolifera</i>	2	T1 & T4	13	NA	0	62
	<i>A. prolifera</i>	3	5	13	NA	0	62
	<i>A. prolifera</i>	16	T3	6	0.12	281	2096
Manatee Channel	<i>A. cervicornis</i>	8	NA	0	NA	0	62
	<i>A. palmata</i>	9	NA	0	NA	0	62
	<i>A. prolifera</i>	7	NA	0	NA	0	62
RockyPoint	<i>A. prolifera</i>	1	NA	12	NA	0	62
	<i>A. prolifera</i>	12	NA	6	0.0667	156	1164

Table 2. Estimated minimum and maximum ages (in years) of clonal populations with at least five ramets (clonal samples), calculated from somatic mutations. Transects are given for samples from Coral Gardens.

Somatic age proportions across study sites

A. cervicornis



A. prolifera



A. palmata

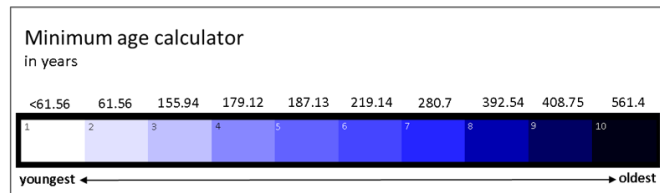


Figure 2. Estimated minimum ages calculated from somatic mutations, represented as proportions. Sample size, n , represents every colony in the population when $n=N$. Numbers in the bars correspond to the color code shown in the minimum age calculator.

genotypic diversity. The low number of *A. prolifera* clones observed also indicates that hybridization rates of the parent species *A. cervicornis* and *A. palmata* are low. Our genotypic diversity calculations are conservative and show lower values than those seen in Baums et al. (2006). The large disparity between Baums' low values and our values is likely primarily due to variation in sampling method. Our sampling method, however, was extremely thorough as large sample sizes from a wide area of the larger reefs were collected, and complete censuses of populations were collected when possible (populations were small enough). Similarly low levels of sexuality seen in neighboring Caribbean populations corroborate the plausibility of our results. *A. palmata* in Mexico shows mostly asexual reproductive behavior, while in Florida it shows asexual reproduction at 2 sites, mostly asexual behavior at 1 site, and mostly sexual behavior at only 1 site (Baums et al. 2006). This similarity is also reflected in report of regional genetic isolation throughout the Caribbean, divided into Western and Eastern genetic intermixing populations (Baums et al. 2005). Our results further endorse the claim in Baums et al. (2006) that Western *Acropora* populations exhibit less sexual reproduction than Eastern.

Genotypic diversity is so low that it cannot be contributing to the high live coral coverage at

Acropora populations at our study sites. At other abundant sites of *Acropora* in the Caribbean, it was predicted that these populations are critical spawning sources of propagules and might help reestablish genetic diversity and coral coverage at neighboring sites (Keck et al. 2005; Zubillaga et al. 2008; Lirman et al. 2010, Vargas-Angel et al. 2003). We provide potentially confounding results, showing that in at least one region (N. Belize), live coral coverage and abundance does not indicate genotypic diversity or spawning potentiality. Direct observation of spawning behavior would need to be observed to confirm the claim that the local *Acropora* are not largely acting as propagule sources. Due to large surface area of clones at many sites, it remains possible that larvae production occurs but cannot successfully fertilize because of self-incompatibility (Baums et al. 2005; Coffroth and Lasker 1998).

High degrees of clonality can be detrimental to reef populations in the event of continued or worsening environmental conditions or pathogen attack (Schmid et al. 1994; Steinger et al. 1996; Reusch et al. 2005; Walker et al. 2008), thus the current live coral cover and spread seen at our sites is vulnerable to future compromise. This combination of low genotypic diversity and high abundance begs the question of the relative importance of fecundity and population growth rate. Negative relationships between life span and genotypic variability have been shown in clonal plants, as well as large temporal population fluctuation in new clones less developed in size (Garcia et al. 2008). Long lifespans associated with larger sizes are predicted to be good buffers against population fluctuations because of physical stability in the habitat (Garcia et al. 2008). These thriving veteran populations, or *refugia*, may have resisted extinction due to their high compatibility with the environment and due to their ability to absorb or rebound from disturbances (Eriksson et al. 2000; Riegl et al. 2009). While clonal stability is not believed to mitigate the need for sexual reproduction (Eriksson et al. 2000), variation within large clonal populations exists. Competition among individuals of a clone may maintain genotypic diversity and allow for adaptation to an environment within a clone as opposed to among genets (Soane and Watkinson 1979; Hara et al. 1994; van Kleunen et al. 2001; de Witte et al. 2010).

While common among clonal species in nature, a positive relationship between age and abundance cannot be assumed in all communities. In some cases, largely abundant populations can be fairly recent and proliferated quickly due to fast growth rates (Garcia et al. 2008). In order to determine if the populations observed at our sites are veteran populations or new, fit clones, genotypic diversity and age data must be considered together. Coral Gardens shows a wide range of ages across *Acropora* populations, suggesting the possibility that bottleneck and/or founder effects took place. At Manatee Channel *Acropora* populations are all completely new. The single genet of *A. prolifera* indicates that a founder effect took place in which one parent populated the entire area, while *A. cervicornis* and *A. palmata* clonality also indicates founder effect occurrence but by more than one parent. At Rocky Point the *A. prolifera* populations are a combination of relatively new and old, indicating a possible combination of founder and bottleneck effects.

Results also potentially confound previous claims that *A. prolifera* expansion is a recent event in the Caribbean. It has previously been thought that *A. prolifera* only recently emerged to inhabit substantial surface area (Willis et al. 2006, Fogarty et al. 2010, Richards et al. 2015), but results here suggest that in Belize it has existed for longer than expected, in locations at Rocky Point for between 0-156 years and Coral Gardens for between 0-281 years. Our data suggests that new *A. prolifera* colonies exist with the ability to cover large areas, but that the hybrid has existed in some locations for a long time.

Overall, this study provides data suggesting that *Acropora* populations in Northern Belize sites are largely clonal and reproduce primarily by fragmentation. Furthermore, the ages of these populations range from new to relatively old, suggesting a combination of refuge populations and new recruits. Among some of these older populations are colonies of *A. prolifera*, indicating that this species has potentially existed in this region longer than previously expected. It is our hope that these results will help the coral reef community to better understand the dynamics of some of the last remaining abundant *Acropora* reefs.

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