The Meaning of Success in Caribbean Acroporid Restoration: The First Eight Years' Results from Belize

El Significando del Éxito en la Restauració de Acropóridos del Caribe: Resultados de los Primeros Ocho Años en Belize

Le Sens De La Réussite dans les Caraïbes Acroporid Restauration : Les Résultats de Belize Des Huit Premières Années

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ABSTRACT

Coral restoration efforts have become accepted widely as an active management tool but still lack a realistic sense of scale, achievable goals, and success indicators. Since the Caribbean acroporids are listed by the IUCN as 'Critically Endangered', a general goal of restoration efforts is to prevent their extinction. More specific goals are to restore lost ecosystem services like shoreline protection, fisheries enhancement, biodiversity preservation, and provisioning of aesthetic and economic services for the tourism industry. Continuity is key to ecosystem service values, which requires that the restored coral community be (1) self-sustaining and self-propagating, and (2) resilient against persistent insults. Genetic diversity must be addressed regardless of propagation methods (sexual versus asexual). Longevity may be increased by identifying coral genotypes that are resilient to thermal stress, disease and/or predation. How much genetic diversity is needed? What amount of coral coverage, and placed where, is needed to trigger natural regenerative processes at larger scales? Presented here is eight years of acroporid restoration efforts at Laughing Bird Caye National Park, Belize, where over 11,000 nursery-grown acroporid fragments have been out-planted. Data were acquired on host and algal clade diversity, rates of growth and survival, bleaching history, reproductive (spawning) indicators, methods for measuring live coral cover over time, methods to assess changes in fish biomass and species composition on out-planted sites, and mechanisms to include local community members in the work. We suggest realizable goals and success indicators, offer guidance for expanding restoration efforts to new sites, and recognize Marine Protected Areas as key to coral restoration.

KEY WORDS: Coral restoration, Caribbean acroporids, genetic diversity, success indicators, ecosystem services

INTRODUCTION

Scientists have observed a precipitous global decline in live hard coral cover on the world's coral reefs (Carpenter et al. 2008, Wilkinson and Souter 2008), in response to which coral restoration has become widely accepted as one of several important active management tools (Jaap et al. 2006, Baums 2008, Baums et al. 2010). Various types of *in situ* coral nurseries, often incorporating methods for coral husbandry and propagation developed in the marine aquarium trade, have proven effective (Lirman et al. 2010, Johnson et al. 2011, Bowden-Kerby and Carne 2012, Young et al. 2012, Lirman et al. 2014, Rinkevich 2014). In the Caribbean, the focus has largely been on members of the scleractinian family Acroporidae as these were the first coral species listed by the IUCN as Critically Endangered, and because they were previously among the most abundant shallow-water reef-building species in the region (Aronson et al. 2008). The Caribbean acroporids have been labeled keystone (Lirman et al. 2014) or foundation species (Kreyling et al. 2011) due to the ecosystem services that the provide, including shoreline protection, habitat for hundreds of other marine species, and socio-economic value from tourism and fisheries. In addition to their inestimable non-market existence, cultural, and aesthetic values, coral reefs in the Caribbean alone have been assessed in purely economic terms at US$5-11 billion/year (IPCC 2007) and in Belize, the country of this research, at US$268-370 million/year (Cooper et al. 2008).

Acroporid restoration projects in the Caribbean have given us decades of field data and experience; however the emphasis, especially for the US territories, was historically on discreet, one- time, one-reef restoration efforts in response to physical damage such as a ship grounding or other isolated anthropogenic impact events (Miller 2000, Jaap et al. 2006). Much of the criticism of coral restoration efforts centers on their small-scale, and by definition, their lack of significance relative to their high costs (Precht et al. 2005).

As live acroporid coral cover continues to decline in most of the Caribbean (Jackson et al. 2014, Rodríguez-Martínez et al. 2014), discussions have shifted from restoration as a tool for discreet short term reef recovery to methods for species recovery, survival, and long-term adaptation to rapidly changing conditions due to an amalgam of global climate change and intensified local human impacts (e.g. increasing temperature, decreased ocean pH, high nutrient loads, overfishing, disease, increasingly violent storm events, etc.) (Kreyling et al. 2011, US National Marine Fisheries Service, 2014). Debates still rage over the relative threat level posed by each of these stressors, alone and in combination (Jackson et al. 2014). Many argue that without changing the external environmental conditions that led to these species' regional decline, restoration efforts are futile (Precht et al. 2005). Others argue that without knowing these species' original genetic diversity, their populations may have already bottlenecked to some degree (Kreyling et al. 2011), and restoration efforts using asexual fragmentation may unknowingly contribute to inbreeding depression (Omari 2011). Though voluminous, the literature suggests a lack of a coherent, sophisticated understanding of what has happened to coral reefs or what might be done about it.

Complicating these discussions are the still unknown relative roles of the symbiont versus the host genetics of the coral holobiont as these relate to growth, morphology, and thermal tolerance, with new information on both gathering rapidly

(Baums et al. 2014, LeJeunesse et al. 2014). Publications abound on acclimatization versus adaptation in short-term studies conducted primarily in the Indo-Pacific, and typically on juvenile and/or lab-reared corals (Jones and Berkelemans 2010, Oliver and Palumbi 2011, Howells et al. 2013, Humes et al. 2013).

Despite these unanswered questions, acroporid nurseries in the Caribbean have proliferated in recent years, with most publications still remaining focused on growth and success in the nurseries alone, with little attention to the long term survival and growth of second generation out -plants (Howells et al. 2013, Lirman et al. 2014); one notable exception is a study of out-planted corals in Japan (Omori, 2011). While several publications list *criteria for success* (Miller 2000, Jaap et al. 2006), until the recent release of the Draft Recovery Plan for Elkhorn and Staghorn Corals (US National Marine Fisheries Service 2014) these criteria were couched in vague terms such as, *performance of a restoration project is considered satisfactory if the biological attributes meet or exceed those of the reference sites* (Japp et al. 2006), especially since the utility of reference sites is compromised by the continued decline of Caribbean acroporids in many places.

Here, we present data on more than 11,000 second generation out-planted acroporids at Laughing Bird Caye National Park (LBCNP) in southern Belize, with work ongoing since 2006. We have attempted to address genetic diversity in the work, and continue tracking growth, survival, and thermal tolerance of specific host-symbiont pairings on both Caribbean acroporid species as well as their ecologically important hybrid. In this report, we share our methods for assessing long-term growth and for tracking the interspecific relationships and cascading recovery processes that compound and accelerate as we rebuild reef-surface communities and restore reef-building fabrics. We suggest that this eight-year study is a successful example of acroporid restoration, redefined as assisted re-colonization and restored sexual reproduction. We view the outcomes of restoration as a form of climate change adaptation, based upon reintroduction and reestablishment of pre-adapted ecotypes to sites where they were formerly dominant. Furthermore, we begin to address the lack of published work on long-term survivorship and growth in corals relocated from one reef to another (Carne 2008, 2011, Howells et al. 2013) and from nurseries to reefs (Omari 2011, Bowden-Kerby and Carne, 2012, Lirman et al. 2014). The work focuses on restoring *Acropora* corals to Laughing Bird Caye National Park, a large and reasonably effective no-take area in Southern Belize where formerly abundant and structurally dominant acroporids had completely died out in recent years.

METHODS

The first 19 *A. palmata* fragments transferred to LBCNP in 2006 were *fragments of opportunity* (Monty et al. 2006) from Gladden Spit and the Silk Cayes Marine Reserve (GSSCMR). Out-plant site justification, donor reef genetics (Baums et al. 2006, Carne 2011), out-planting methods and locations, and one-year growth measurements using marked branches (Shinn, 1976, Carne 2008, 2011) of out-plants and controls are published (Carne 2008, 2011). Regular monitoring includes photographs and field notes on bleaching (Lang et al. 2007), etc. on these initial transplants and has continued (2006-present).

In-situ nurseries (two table nurseries and six frame nurseries) were established in 2009, in and around LBCNP, and were stocked with 17 acroporid genotypes representing *Acropora cervicornis*, *A. palmata*, and their hybrid *A. prolifera* (Bowden-Kerby and Carne 2012). These 17 acroporid genets, along with six of the transplanted *A. palmata* (n = 23), had their coral host genetics analyzed by microsatellite markers to ensure they were different from each other (Baums et al. 2006, Bowden-Kerby and Carne 2012). The 23 acroporids also had their symbiont clade identified using ITS2-DGGE methodology (Sampayo et al. 2009) and quantitative qPCR (Bowden-Kerby and Carne 2012). In 2010, mapping of extant acroporid stands (Carne 2011) continued and an additional 50 acroporids had their symbiont clade identified. Of these, one *A. cervicornis* genotype housing clade D1a, *Symbiodinum trenchii* (LeJeunesse et al. 2014) was added to the nurseries and out -plants in 2010.

Relative growth in the nurseries was measured using AGRRA methods (Lang et al. 2007) for the corals in the frame nurseries and maximum linear extension rates were measured for the *A. cervicornis* genets on ropes suspended from metal tables (Bowden-Kerby and Carne 2012). Growth data were collected again for *A. cervicornis* housing either symbiont clade A3 or *S. trenchi* on ropes in the nurseries in 2012 using maximum linear extension, and in 2013 using Total Linear Extension (TLE, Kiel et al. 2012, Carne and Cho-Ricketts 2014).

Monitoring for bleaching in the nurseries and on the out-plant sites uses the AGRRA methods (Lang et al. 2007). *In situ* temperature data were collected with Hobo U -22 loggers, with data uploaded every year.

Out-planting nursery-grown corals was done primarily with cement, but also some wedging of fragments without cement, and some pegged ropes, each containing multiple fragments entwined in the ropes. These were planted directly on to the reef and secured with concrete nails (Bowden-Kerby and Carne 2012). Out-planting to date has occurred in 22 sub-sites around LBCNP, numbered chronologically, with data on sub-site area, number of each species/genotype/clade and out-plant method recorded.

Video-mosaics (Lirman et al. 2007, Gintert et al. 2012) have been completed on six plots at three different status/ age of out-plant sites at LBCNP. Areas for each plot were calculated by physically measuring the plots sizes after installing semi-permanent corner markers and using transect tape for perimeters and diagonal length measurements.

RESULTS

Eighteen of the original nineteen *A. palmata* fragments of opportunity transplanted to LBCNP in 2006 are still surviving and continue to be monitored regularly; one small fragment mortality occurred in the first year after transfer (Carne 2011). Storm and/or fin damage has created several (> 10) additional satellite colonies, some of which have been reattached by divers and others have self-adhered to the substrate; these are not counted in the

numbers of out-plants shown yet represent natural asexual propagation.

Second generation corals were trimmed from the eight nurseries and out-planted in 2010 (Bowden-Kerby and Carne 2012). Three additional dome nurseries were installed with *A. cervicornis* in 2012 to test a new method and additional table nurseries were installed bring the total to 13 table nurseries in 2014, each supporting rope culture of *A. cervicornis* and *cement cookie* culture of *A. palmata*.

The total number of out-planted acroporid fragments at LBCNP is now 11,021. These are planted in 22 sub-sites fringing LBCNP (Figure 1a,b). Data are kept on species, mother colony origin, clade identification (if known), nursery culture method, out-planting technique, and survivorship. The increasing number of corals out-planted each year is a reflection of funding, increased number of nurseries, and improved out-planting techniques (Figure 2a). The spacing between the sub-sites and mixing of genets for each species was decided in discussion with Baums (personal communication 2009) to maximize the potential for successful sexual reproduction.

Figure 2b illustrates the number of each acroporid species out-planted. Although the original emphasis was on *A. palmata* transplants, the faster growth and ease of culture success is why there is exponentially more *A. cervicornis* out-planted at LBCNP; this species, like the *A. palmata*, naturally regenerates after storm and human damage, but the prolific numbers of branches make this impossible to quantify by counting.

Host genetics were analyzed in 2009 on all 23 acroporids in the nurseries to quantify their diversity (Figure 3a) and their *Symbiodinium spp.* were identified to the sub-clade level (Figure 3b.) (Bowden-Kerby and Carne 2012). In 2010, an additional 50 acroporid genotypes were mapped and sampled for their symbiont clade identification; one of these inner reef-sourced *A. cervicornis* genets was found to house *S. trenchii* and this coral has been included in the nurseries and out-plant sites since 2010. Of the 73 acroporids thus far sampled, only one outer-reef sourced coral (an *A. palmata*) housed D1a. This is reportedly a more thermally tolerant *Symbiodinium* species. This coral has thus far not been included in the nurseries and so was not included in growth rate studies (Figure 4), but is mentioned to highlight the ongoing efforts to identify and incorporate more diversity into the restoration work.

Initial comparative growth rate studies in the nurseries have revealed notable differences attributable to both coral genotype and nursery location (depth) (Bowden-Kerby and Carne 2012). In general, the inner-reef sourced genets grew faster than the outer-reef (GSSCMR) sourced corals (Figure 5). The outer-reef sourced corals in the nurseries

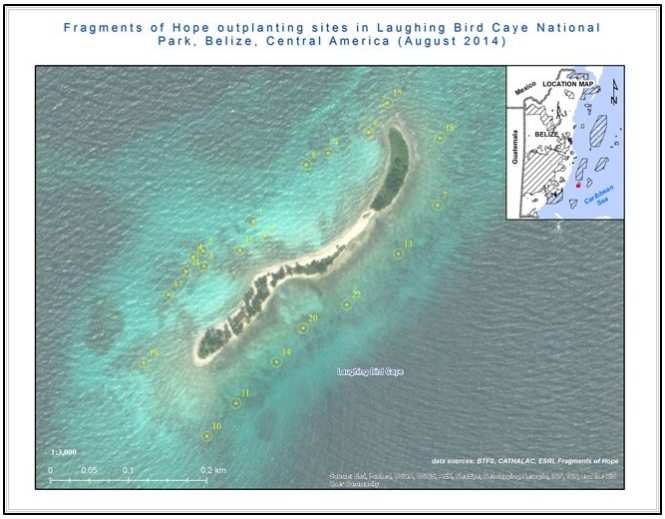

Figure 1b. Newest map created with actual GPS coordinates and accurate scale. The MPA layer is sourced from Belize Tropical Forest Studies (BTFS), a local NGO.

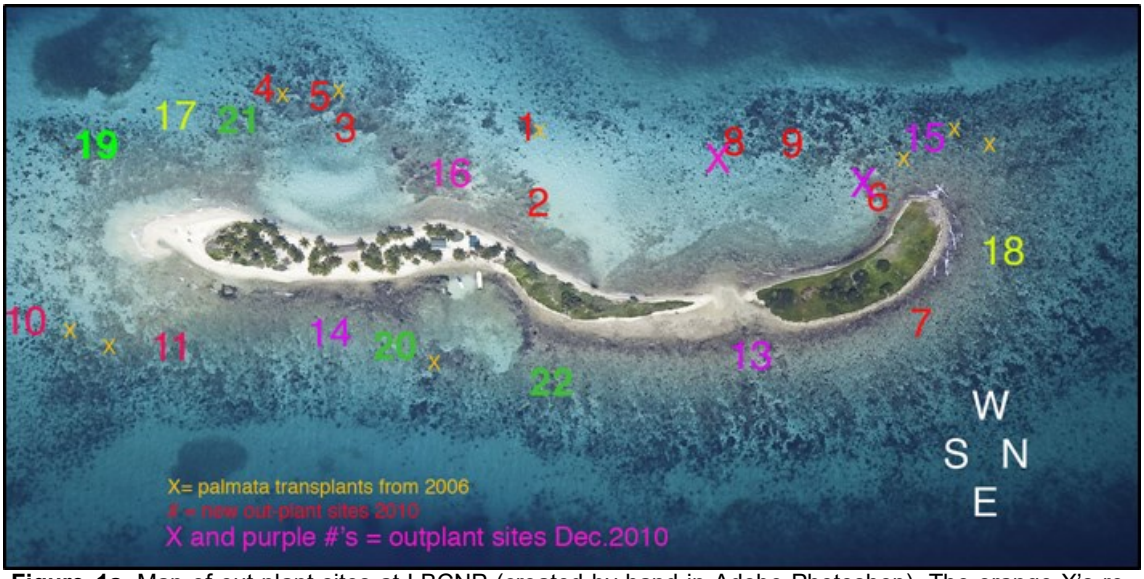

Figure 1a. Map of out-plant sites at LBCNP (created by hand in Adobe Photoshop). The orange X's reflect the first 2006 transplants, the red numbers (1-11) reflect sites added in 2010, the yellow numbers (17 and 18) illustrate sites added in 2011 and 2012, respectively, and the green numbers (19-22) are sites added this year, 2014.

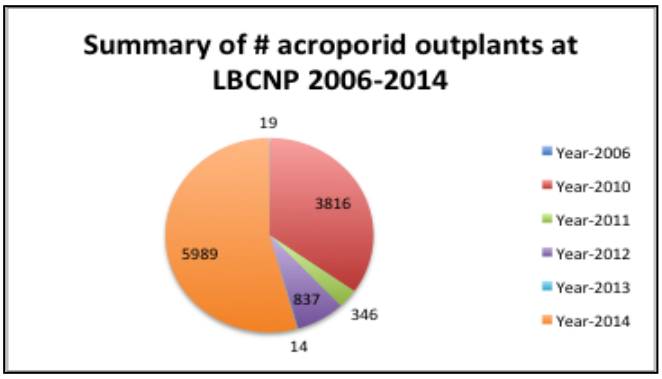

Figure 2a. Number of acroporid corals out-planted at LBCNP by year.

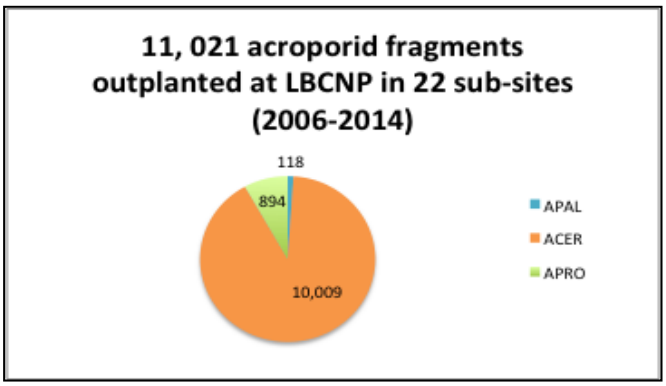

Figure 2b. Number of acroporid corals out-planted at LBCNP by species.

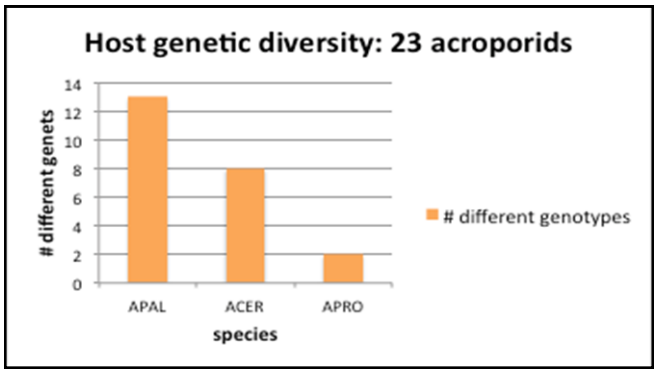

Figure 3a. Thirteen *A. palmata,* eight *A. cervicornis* and two *A. prolifera* genets are known.

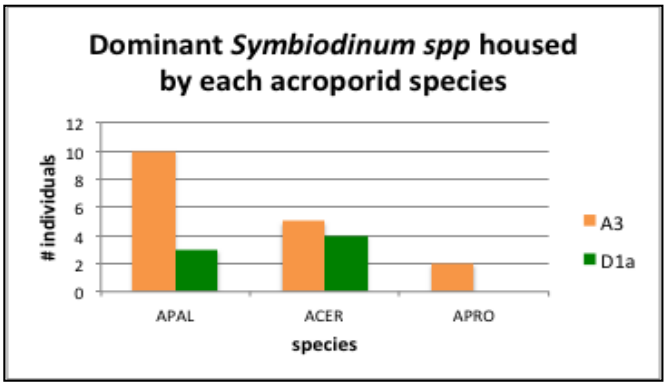

Figure 3b. Ten *A. palmata*, five *A. cervicornis* and both *A. prolifera* genets house clade A3.

only housed clade A3, and because the inner-reef sourced corals housing D1a appeared to grow faster than the inner-reef sourced corals housing clade A3, growth rate experiments were repeated again in 2012 and 2013 with more specific methodologies so statistics could be applied. In both studies, using different amounts of *A. cervicornis* genets and different methodologies to measure growth rates, the corals housing *S. trenchii* grew significantly faster than the corals housing Clade A3 (Figure 6 Carne and Cho-Rickettes 2014)

Growth rate studies, while not simplistic for acroporids because of their branching, three-dimensional morphology, can be accomplished in the nurseries on small fragments (Kiel et al. 2012, Lirman et al. 2014). However, measuring growth rates of larger, mature colonies, and multiple colonies, is impossible with the same methodologies as those used in the nurseries.

A video/photo-mosaic technique has been developed to measure live, mature coral cover at a larger scales (Lirman et al. 2007, Gintert et al. 2012) and can be repeated over time to estimate rate of increased coral cover. Six mosaics have been completed at LBCNP on three different ages of nursery-grown coral out-plant sites, in two replicates: unplanted, six-months planted and four years planted (Table 1, Figure 7). One replicate for each aged mosaic is on both the lee- and windward sides of LBCNP. Initial results are housed at:

http://web2.physics.miami.edu/~agleason/mosaic_results/belize_acropora/index.html.

While acroporids reproduce both asexually and sexually, and it is unknown which method is predominant for each acroporid species and each locality; by definition only sexual reproduction can contribute to genetic diversity and long-term adaptation. Four different *A. cervicornis* genets from four different out-plant sub-sites at LBCNP were sampled in 2012, prior to predicted spawn dates. *A. cervicornis* housing either *S. trenchii* or Clade A3 were represented. All were out-planted just under two years prior to sampling. These were stained and examined histologically by Dr. Peters at George Mason University and revealed mature gametes (Figure 8): *The large roundish pink-red with white spots objects are mature ova. They are beginning to separate from the mesoglea, meaning they will be released soon. The dark purple spotted; with streaks of red, structures are spermaries. Each tiny purple dot is a spermatozoan with red flagellum attached, meaning they will be released soon, too*. Only *A. cervicornis* were sampled.

Visual confirmation of nursery-grown out-planted *A. cervicornis* also occurred one day after the full moon in August 2014. A single *A. cervicornis* colony spawned 9:10 pm on August 11, 2014, representing less than 5% of all the colonies (same genet, same age) at that sub-site. Out-planted acroporids were monitored August 10-14, ~8-10 pm each night and no other spawning was observed.

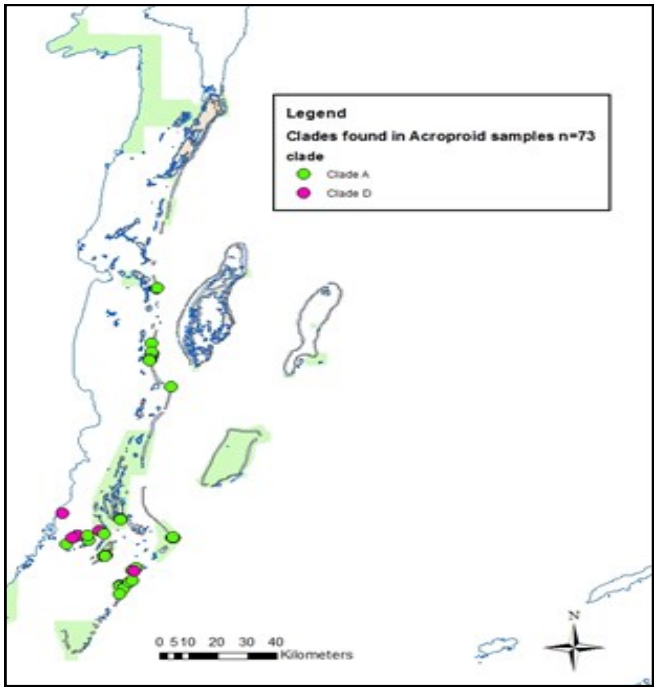

Figure 4. Distribution of clade types in 73 in 73 acroporid corals sampled.

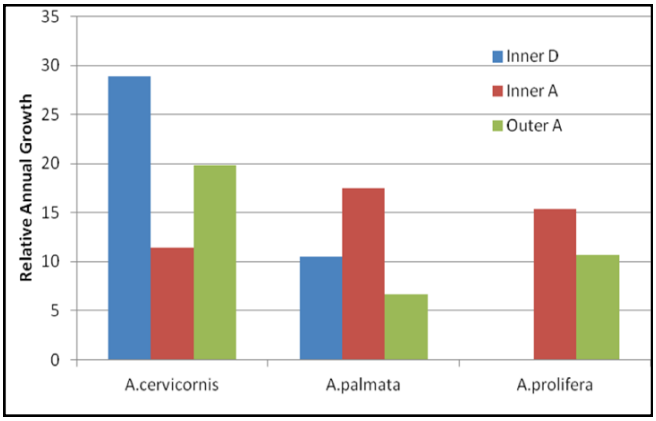

Figure 5. Inner-reef sourced corals grew faster than outer-reef sourced corals; one year in the nurseries (Bowden-Kerby and Carne 2012).

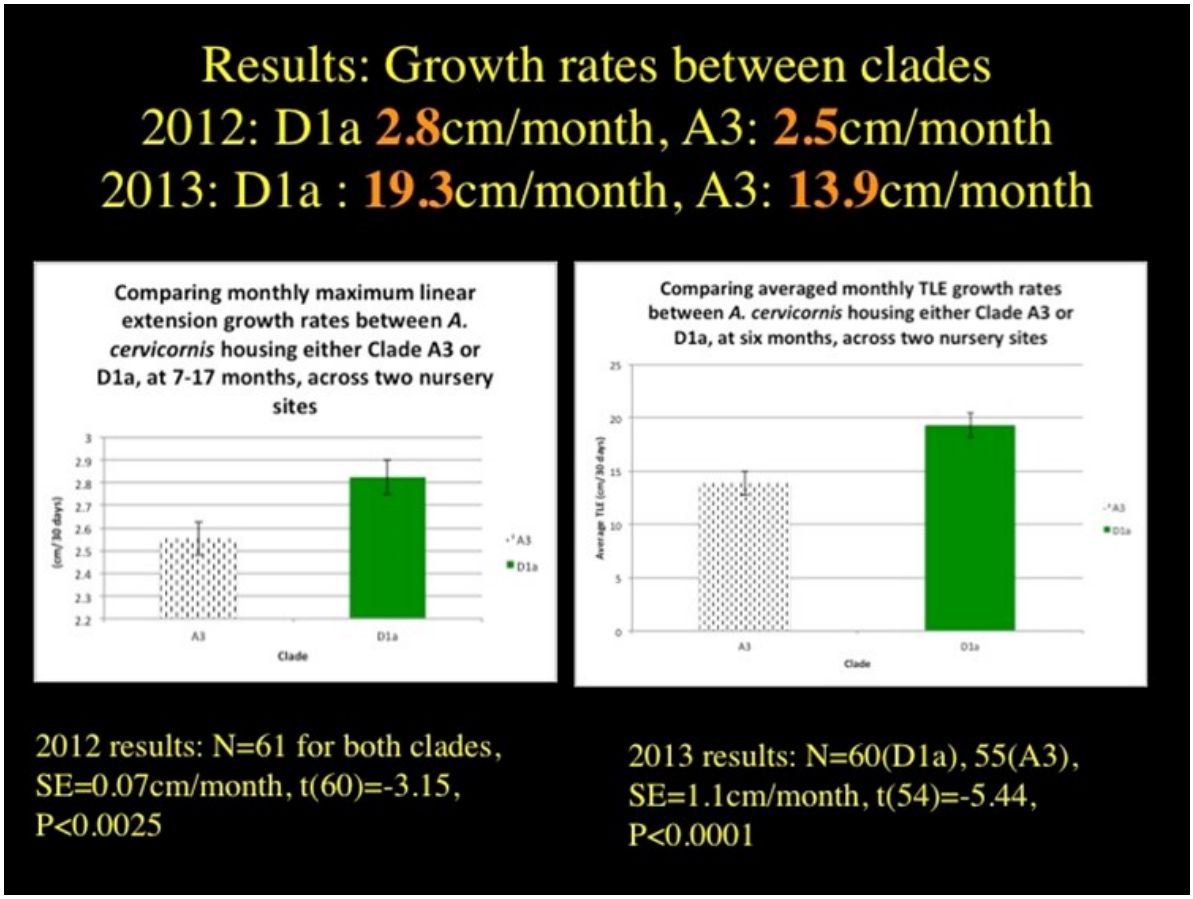

Figure 6. Two different studies both revealed that *A. cervicornis* housing *S. trenchii* grew significantly faster than those housing Clade A3 in the nurseries.

Table I. Sub-site label, areas, date out-planted and species out-planted at each of the six mosaic plots at LBCNP. (Figure1a-b illustrates sub-site locations except UP1 and 2).

Site/plot name	Area (m^2)	Out-plant date/status	Species out-planted
13	182	December 2010	ACER, APAL, APRO
9	110	April 2010	ACER
20	144	February 2014	ACER, APAL, APRO
21	109	February 2014	ACER, APAL, APRO
UP 2	112	unplanted	N/A
UP 1	40	unplanted	N/A

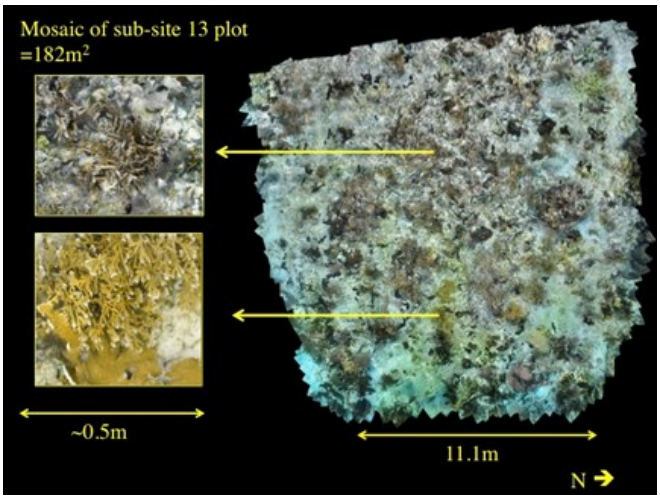

Figure 7. First results of one of the mosaic plots at LBCNP.

DISCUSSION

Goals for coral reef restoration may be stated at the level of site or community, species or assemblage. Nonetheless, it is entire regional coral reef communities that are most at risk, not just - and perhaps not even at all - the individual species. In the US the strongest environmental law regulating threats relevant to coral reef recovery is the Endangered Species Act, under which the Caribbean acroporids in US waters are listed as threatened. The IUCN Red List places a similar emphasis on the continued existence of individual species. Over-reliance on the ESA (as by the Center for Biodiversity in a recent push for the listing of 82 coral species as Endangered) sets up a mismatch between the actions interventions actually required for system recovery, and the legal mechanisms available to effect it. The recent draft Recovery Plan for Elkhorn and Staghorn corals (US National Marine Fisheries Service 2014) has the most specific restoration goals yet published and these are species-based. The authors suggest a coral cover of 60% for elkhorn and 25% for staghorn to be re-established in at least 10% and 5%, respectively, of their historical range. Considering a practical spatial scale of individual 100 m^2 restoration patches within a recovery site, we suggest aiming for reestablishment of a self-sustaining, combined acroporid species coral cover of 35 - 50% within the reef habitats that corals of this genus historically dominated. This target

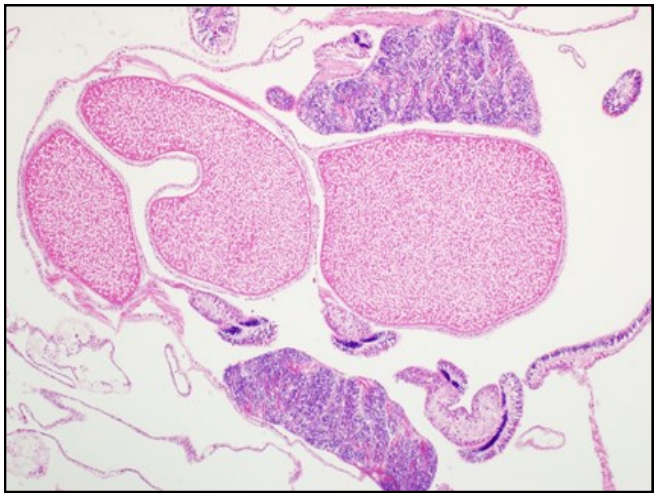

Figure 8. Histological evidence of sexual reproduction in nursery-grown *A. cervicornis*, out-planted in 12/2010 and sampled in 07/2012.

seems feasible from the standpoint of production, out-planting, and monitoring, and is consistent with a rational broader goal of recovering the mixed *Orbicella – Acropora* accretional fabric that constitutes the structural backbone of core coral reef habitat over most of the west Atlantic shallow water domain. The progress of selected 100 m^2 patches can be tracked quickly, accurately and in great detail with orthogonal high information-density video-photo mosaics taken over time at each target site.

Enrichment and/or maintenance of the diversity of locally adapted holobiont genets (minimally, meaning the coral hosts plus symbiotic dinoflagellates) is another meaningful criterion for successful restoration. For both acroporid species, the draft Recovery Plan advises a genetic (host) ratio (genets to colonies) of $\geq$ 0.5. We measured a ratio of 0.7 for *A. palmata* host genetic sampling completed in 2007 at the original donor reef site in GSSCMR (Carne 2011), and concur with this goal. Similar within-stand host genetic studies have not yet been completed for *A. cervicornis*, but collaboration with researchers at the University of Miami is under way to address this knowledge gap. To date, there are at least 13[1] different *A. palmata* genotypes out-planted at LBCNP and at least 113 colonies (not including satellite colonies), but these are scattered throughout the multiple sub-sites, which does not yet meet the target goal for host genetics. Future plans and funding have been secured to map, analyze, and add an additional twenty unique acroporid genets to the nurseries and out-plant sites, while continuing to increase the number of out-plants at LBCNP by ~ double (another 10,000 from the existing 13 nursery tables) over the next 12 months.

By continuing to analyze the host identities of new donor genets, culturing them asexually, out-planting the different genets in close proximity (1 - 30 m) and monitoring for spawning activity, we hope we have addressed the need to alleviate the threat of inbreeding depression of genetic diversity (Omori 2011). We recognize that documented sexual reproduction does not translate to

viable recruits surviving to sexual maturity and identify this as another research gap needing to be addressed (Dizon and Yap 2006). However, we feel encouraged by the original *A. palmata* transplants' from one reef (GSSCMR) to another (LBCNP) 95% survival rate over eight years, considering also their natural asexual regeneration success (satellite colonies) from storm events.

The results here show that Caribbean acroporids can be propagated *en masse*, outplanted, and also expected to survive and spread. Ours are the longest survivorship records thus far for nursery-grown corals transplanted to a reef (2010 - 2014) (Omori 2011, Howells et al. 2013, Lirman et al. 2014). More time is required to know if this approach to acroporid restoration will eventually produce a resilient, safe-sustaining, and larval sourcing acroporid canopy, or how achieving this level of success will materially aid in the recovery of the coral reef community as a whole. What we have demonstrated, as revealed by study of symbiont genetics and bleaching vulnerability for up to eight years post-outplant, is the feasibility and practicality of assisted recolonization of an endangered reef foundation species. This success is attributable, at least in part, to having used multiple donor holobionts (Kreyling et al. 2012, Baums et al. 2014).

We were pleasantly surprised to observe only a very low rate of predation (except at one sub-site). This stands in contrast to published observations of high predator-induced mortality during natural recovery of acroporid-dominated habitats such as the fore-reef terrace in Jamaica (Tunnicliffe 1983). We postulate that the low coral predation and high long-term colony survival that we observed is attributable to the long-standing, well-enforced (> ten years) no-take status of LBCNP, bringing this small area ecologically closer to an earlier time in the Caribbean (Jackson et al. 2014). The prevalence of hard-grazing herbivores such as the sea urchin *Diadema antillarum* and the parrotfish *Sparisoma viride* help to explain the relative lack of macroalgae in the shallow reefs (0 - 5 m) around LBCNP (Carne and Kaufman personal observation). A high abundance of spiny lobsters (*Panulirus* spp.) and low abundance of the coraliophagous snail *Coralliophila abbreviata* likely contribute to the low rates of coral mortality and the infrequency of the snail's characteristic kill scars. Extensive monitoring data (MMAS 2005-2010, www.science2action.org, and Kaufman and Shank (personal observation) from the deeper waters of LBCNP, away from the immediate vicinity of the caye, offer an interesting contrast in closely resembling the more degraded condition typical of most of the MesoAmerican Reef system (McField 2011). This is likely due to enforcement being much weaker out of sight of the people-particularly rangers- who frequent Laughing Bird Caye itself. Future research plans include quantitative assessment of fish biomass and community structure, biodiversity inventory of all acroporid inquilines and other species associates, and contingency analysis of colony life history as a function of the surrounding benthic community.

The Acroporid restoration is far from complete at LBCNP, but we do for the first time have quantifiable indices of success (% coral cover increased, genetic diversity, sexual reproduction, longevity, and thermal tolerance) and have identified other indicators and ways to measure them in the future. Results from LBCNP support the legitimacy of expanding acroporid restoration efforts elsewhere in Belize and the wider Caribbean, provided that these remain under close scientific scrutiny and are conducted in an adaptive manner that incorporates experimentation and learning. Our success did not arise in isolation: the project benefited greatly from participation by knowledgeable fishermen, tour guides, local NGO's, and the Belize Fisheries Department, all of whom were involved at every stage (mapping, scoping, establishing and monitoring nurseries, out-planting and monitoring of out-plants) from 2006 through today. In addition to making the restoration work physically feasible, this high level of community engagement is an essential part of the restoration process for it is not only corals that we must seek to restore. Rather, we must also rebuild, or build anew a sense of community engagement, stewardship, and responsibility for the health and future of the ecosystem upon which coastal peoples so depend.

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