Reef-scale trends in Florida *Acropora* spp. abundance and the effects of population enhancement (#10646)

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Reef-scale trends in Florida *Acropora* spp. abundance and the effects of population enhancement

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Since the listing of *Acropora palmata* and *A.cervicornis* under the U.S. Endangered Species Act in 2006, increasing investments have been made in propagating both species in offshore coral nurseries and outplanting cultured fragments to reef habitats. This investment is superimposed over a spatiotemporal patchwork of ongoing disturbances and the potential for natural population recovery. In 2014 and 2015, we repeated broad scale, low resolution Acropora spp. censuses conducted in appropriate reef habitats during 2005-2007 to evaluate the trajectory of local populations and the effect of population enhancement. Generally, *A.palmata* has been the target of much less enhancement effort and has shown small, but often negative changes in reef scale density. Meanwhile, *A.cervicornis* showed a significant increase in colony density at sites where population enhancement had been conducted between 2005 and 2014, with stable or slightly negative trends at sites without population enhancement and a significant correlation of change in colony density with cumulative numbers of prior outplants across sites. Both enhanced and unenhanced sites showed negative trends for both species between 2014 and 2015, reflecting widespread mortality caused by severe thermal bleaching in fall 2014. This study documents a substantive benefit of *Acropora* spp. population enhancement in the Florida Keys against a backdrop of ongoing population decline.

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Keywords: Florida Keys, *Acropora palmata*, *Acropora cervicornis*, GIS, spatial analysis, bleaching, coral nursery, outplanting

ABSTRACT: Since the listing of *Acropora palmata* and *A. cervicornis* under the U.S. Endangered Species Act in 2006, increasing investments have been made in propagating both species in offshore coral nurseries and outplanting cultured fragments to reef habitats. This investment is superimposed over a spatiotemporal patchwork of ongoing disturbances and the potential for natural population recovery. In 2014 and 2015, we repeated broad scale, low resolution *Acropora* spp. censuses conducted in appropriate reef habitats during 2005-2007 to evaluate the trajectory of local populations and the effect of population enhancement. Generally, *A. palmata* has been the target of much less enhancement effort and has shown small, but often negative changes in reef scale density. Meanwhile, *A. cervicornis* showed a significant increase in colony density at sites where population enhancement had been conducted between 2005 and 2014, with stable or slightly negative trends at sites without population enhancement and a significant correlation of change in colony density with cumulative numbers of prior outplants across sites. Both enhanced and unenhanced sites showed negative trends for both species between 2014 and 2015, reflecting widespread mortality caused by severe thermal bleaching in fall 2014. This study documents a substantive benefit of *Acropora* spp. population enhancement in the Florida Keys against a backdrop of ongoing population decline.

INTRODUCTION:

Caribbean coral reefs are home to two species of fast-growing, habitat-forming species of *Acropora* spp. corals; staghorn (*A. cervicornis*) and elkhorn (*A. palmata*). Both are listed as Critically Endangered by IUCN and threatened under the US Endangered Species Act (ESA). Their endangered status accrues from a litany of factors which have caused extensive mortality combined with inadequate recruitment to sustain populations throughout their range. ESA listing carries a legal mandate to 'recover' imperiled species. The Acropora Recovery Plan describes need for ongoing monitoring and evaluation to track the status of populations, as well as the need to curb ongoing threats related to mortality (disease, thermal stress due to global climate change) and proactive population enhancement measures to jumpstart population recovery (NMFS 2015). Substantial effort has built in implementing population enhancement throughout the Caribbean (Young et al. 2012), largely following the 'coral gardening' model (Epstein et al. 2003; Rinkevich 2015). As the *Acropora* population enhancement effort has grown, substantial management and planning effort has gone to foster pursuit of risk-averse strategies. These strategies include de-emphasis of land-based culture and dispersing individual nursery operations to minimize the geographic envelope from which source stocks are drawn and propagated fragments are outplanted, and maximizing and tracking the genotypic diversity of cultured stocks. *Acropora* spp. fragments are propagated via fragmentation in offshore field nurseries, grown to a viable size and then outplanted to reef habitats with the goal of re-creating sustainable population patches which can serve as larval sources to jumpstart population recovery on a broader scale (Johnson et al. 2011).

Unfortunately, the fact that remains that cultured *Acropora* fragments often behave like their wild counterparts in Caribbean reef communities. This means that they are subject to ongoing chronic and acute stressors, often manifesting substantial mortality in the same pattern as the background population (Miller et al. 2014; Schopmeyer & Lirman 2015). Critics of population enhancement maintain that potentially high levels of mortality would preclude any long term benefit to population recovery, and that the level of investment implies that the scale of effect (e.g., area of reef) will remain trivial. Substantial published work has documented the staggering success of these field nursery culture efforts (Griffin et al. 2012; Lirman et al. 2014; Lirman et al. 2010; Lohr et al. 2015) and the short term fate of individual outplants (Griffin et al. 2015; Mercado-Molina et al. 2015). These evaluations are based on tractable observations and measurements of tagged colonies over one to a few years. There is a much greater challenge in evaluating *Acropora* spp. abundance at the meso-scale (100's m^2 to hectares) due to fragmentation, partial, and full colony mortality. Partially as a result, there is no information available evaluating this scale question (namely, can active population enhancement 'move the needle' in affecting reef-scale population trajectories of Caribbean *Acropora* spp.?). We used a broad scale, low-resolution census technique (direct observation by snorkelers documented via handheld GPS; Devine et al. 2005; Walker et al. 2012) to evaluate both the long term (2005 – 2015) trajectory of Florida Keys *Acropora* populations undergoing ongoing acute and chronic disturbances as well as the question of reef-scale impact of population enhancement. These acute disturbances included multiple hurricanes in 2005, a severe cold thermal event in 2010, mild bleaching in 2011, a milder storm in 2012, and a severe warm thermal mass bleaching event in 2014 as well as ongoing and substantial effects of predation and disease (Williams & Miller 2012).

A conservation organization in the upper Florida Keys (Coral Restoration Foundation, CRF) has been propagating and outplanting *Acropora cervicornis* since 2003 (substantial numbers since 2011) and *A. palmata* since 2012 (substantial numbers since 2014), although the number of outplants placed on the reef has varied greatly over time according to the factors such as permitting restrictions, damaging storms which required time for recovery of nursery infrastructure and cultured stocks, and funding levels. This long and sustained effort combined with the availability of historic census information from a range of reef sites in the upper Florida Keys provides a novel opportunity to evaluate potential reef-scale effects of *Acropora* spp. population enhancement against a backdrop of ongoing chronic and acute disturbances in the reef environment. We compared trajectories of *Acropora* spp. density at reef areas which had versus had not received population enhancement efforts over appropriate time frames to evaluate the reef-scale impact of enhancement. We also compared between censuses of each site over longer term (2005/6 to 2014) and the recent severe bleaching interval (2014 versus 2015) to provide a broad assessment of population trends and acute bleaching impacts on *Acropora* spp. populations in this region.

METHODS:

Sites targeted for this study were originally chosen (2005) prior to the onset of substantial population enhancement efforts. Habitat maps (Lidz et al. 2006; Marszalek 1977) were used to identify shallow (< 5m) coral habitat areas in the upper Florida Keys. Targeted reef areas were restricted to less than 5m deep as observations at deeper depths on snorkel become less reliable. This depth range encompasses the core habitat for *A. palmata*, though *A. cervicornis* traditionally occupies a wider depth range. Most sites were surveyed once in 2005-7, once in 2013 or 14, and once in 2015 (Suppl. Table 1; Miller 2008; Williams 2013).

Teams of two or three snorkelers addressed each reef area with the intent to observe the entire reef surface via swimming sequential, parallel linear transects. The width of each transect was adjusted according to site conditions including depth, relief and water visibility, with the intent that the benthos was thoroughly observed with minimal overlap. In practice, this is very challenging to accomplish and several practices were implemented as the effort progressed to improve the practical coverage, including the delineation of the target area (or subset assigned to an individual snorkeler) with weighted dive flags, the use of compasses and pre-agreed headings (generally following the direction of reef spurs) to maintain parallel tracks. In the early censuses, dive scooters (SeaDoo VS Supercharged) were used, but snorkelers performed surveys predominantly under their own power in 2013-15.

Each snorkeler towed a handheld GPS unit (Garmin GPS72 in 2005-7; Garmin eTrex20 for 20113-15) in a waterproof plastic pouch attached to a floating dive flag. The GPS recorded the ‘track’ traversed by the snorkeler. When an *Acropora* spp. colony was encountered, the snorkeler recorded a waypoint on the GPS for each, and recorded the species for each waypoint on a field data sheet. In some cases, *A.palmata* colonies were observed growing in high density patches wherein it was not feasible to demarcate individual colonies. In these cases, the snorkeler would swim around the perimeter of the feature and record waypoints along the outline which were designated on the data sheet as a thicket. The area occupied by designated thickets was examined over time.

After a survey was completed, the GPS-recorded track was saved. Waypoints and tracks were downloaded to a personal computer after each day of censusing and exported to a spreadsheet file, where the waypoint attributes were entered from the field data sheet. For each study site, maps were created in ArcGIS plotting the colonies and thickets observed for each census year (Fig 1A-1C). Lastly, the observational paths followed by the surveyors (i.e. the GPS tracks) were imported to each map to depict the area searched. Using the *Minimum Bounding Geometry* tool, the minimum area covered by the observational path (Observed area) was determined for each year*site map.

For each site, maps were then merged to make temporal comparisons for reef scale density trends; a long-term interval from the periods 2005-07 to 2013-14 (Fig 1D), and a short term interval from 2014 to 2015, over a severe thermal stress event in summer 2014 (Fig 1E). Each temporal comparison was restricted to congruent observed areas of the reef (i.e., covered by the observational tracks in both time points) by clipping the area of comparison to the area of overlap in the observed area for each year using the Intersect tool. If the congruent area consisted of numerous overlapping polygons, then the *Merge Polygon* tool was used. The area outlined as *A.palmata* 'thicket' was calculated at each time point and the number of colonies in each thicket was estimated using a standard density estimate of 1 colony per m^2 (based on independent field estimates using fixed area belt transects at Horseshoe reef over four years yielding a mean of 1.01 $\pm$ 0.26 SD colonies per m^2; M.Miller unpublished data). Individual colony waypoints and thicket abundance estimates were summed for each species to obtain the total abundance for each survey year in the overlapping comparison area. This number of colonies of each species in each year in the congruent search area of reef was converted to density (total number of colonies observed / congruent observed area of reef (m^2)) to compare between time points (Mann-Whitney Rank Sum tests). For temporal comparisons, the proportional change in density between two time points was calculated.

Information on the total number of coral fragments of each species outplanted to each censused reef site by year was provided by staff of the Coral Restoration Foundation (J. Levy and K. Ripple; Pers comm). CRF is the only organization undertaking large scale *Acropora* spp. population enhancement in this region. The change in mean density over the longest observed interval for each reef (Suppl. Table 2) was used to evaluate the overall impact of population enhacement for *A.cervicornis* as outplanting has been ongoing for this species since 2008 and this enabled the use of information from all sites (n=14, a few of which had not been surveyed in 2013 or 14). However, substantial outplanting was only conducted for *A.palmata* since 2014 so the 2014 to 2015 interval only was used to evaluate outplanting effect for this species. For each species, we conducted a Mann-Whitney rank sum test comparing proportional change in colony density between the sites which had and sites which had not received outplants over the relevant interval. Also, a simple linear regression was performed for each species between the proportional change in colony density and the cumulative number of outplants among all sites.

RESULTS:

The total surveyed area for each interval ranged from 55 to 77 hectares while the congruent observed area of reef for temporal comparisons within each site ranged from 1.6 to 15.5 hectares (Table 1). *Acropora palmata* thickets were observed at four sites in 2006-7, two of which had disappeared by 2015. At these two sites (Grecian Rocks and Watson's Reef) the aggregation of *A.palmata* colonies in the thicket area had dwindled to where it was no longer designated a thicket, though a few remnant colonies remained. One of the other two thickets showed approximately half decline in area, whereas the last was approximately stable in area (Fig 2). Overall, this represents over two thirds loss in total *A.palmata* thicket area among these four sites.

In the interval from 2006 to 2014, *A.cervicornis* showed a substantial positive change in density when averaged across all surveyed sites (n=9) with the most dramatic changes occurring at sites receiving outplants (Table 1A, Fig 3A). In contrast, *A.cervicornis* density was essentially stable on average between 2014 and 2015 (co-incident with a mass thermal bleaching event and a smaller cumulative number of outplants) yielding a significant difference in density change between the two intervals (Mann-Whitney Rank Sum Test p=0.024; Table 1, Fig 3A). Meanwhile, *A.palmata* showed much smaller proportional changes in density (corresponding with much fewer total outplants; Table 1, Fig 3). While the average trend was substantially negative in the 2006-14 interval and essentially stable in the 2014-15 (bleaching) interval (Fig 3), this difference was not statistically significant.

To specifically evaluate the hypothesis that outplanting effort had a significant, landscape-scale effect on colony density, we performed two separate tests; for *A.cervicornis* these tests were applied to the full interval of observation at each site (2005-2015, n=14 sites, Suppl Table 2) whereas for *A.palamta*, substantial enhancement effort has only occurred since 2014 so the 2014-2015 interval was used. A Mann-Whitney U-test indicated that sites receiving *A.cervicornis* outplants had significantly different change in density than those that did not (p=0.004). However, no significant difference occurred for *A.palmata* (corresponding to a much smaller cumulative number of outplants, Table 1). Simple linear regression showed a strong and highly significant relationship between change in *A.cervicornis* colony density and cumulative number of outplants among sites (Fig 4A). The similar regression for *A.palmata* for the 2014-2015 interval when outplanting (as well as the bleaching event) occurred showed no relationship (Fig 4B).

DISCUSSION:

Our low resolution but large scale survey approach was repeated over multiple reef sites over a decadal time frame in which both extensive population enhancement effort and an acute thermal disturbance (along with several lesser disturbances) occurred. Thus, this approach was designed to detect large changes at a large spatial scale. Our surface-based observation method restricted mapped areas to less than 5m depth. Although the historic core habitat of *A.cervicornis* likely extended deeper than this, current known distribution of *A.cervicornis* in the Keys is predominated by nearshore (shallower) habitats in contrast to the deeper fore-reef habitats historically described for this species (Miller et al. 2008). Thus, although extensive *A.cervicornis* distribution in deeper areas not covered by our study is possible, current evidence does not support this in the Florida Keys.

Much greater overall enhancement effort went to *A.cervicornis* in comparison to *A.palamta*, and this added effort corresponded to a significant landscape scale effect. *A.cervicornis* showed a significant and positive relationship with the degree of this enhancement effort across sites over the entire study period (Fig 4A). However, the acute thermal bleaching event appears to have overcome even the enhancement effort and yielded no discernable change between 2014 and 2015 (Fig 3) in spite of ~ 1500 outplants occurring across the surveyed sites. Both the overall densities and the scale of the enhancement effort have been smaller for *A.palamta* (Table 1) which shows a clear pattern of declining density over the recent decade both overall (Fig 3B) and as represented in the occupation of thickets (Fig 2). This mostly negative population trend has not been substantively overcome by the small outplanting effort to date.

The resolution of our survey technique was low, as the challenge of a snorkeler navigating in open ocean as well as variation in depth, visibility, and likely individual observer variation yielded less than perfect observational coverage and detection of colonies that were present. However, we implemented improved field techniques over time which improved the operational coverage of the area surveyed (e.g. the deployment of surface markers to delineate the survey area for each surveyor and the use of compasses) over time (e.g., compare coverage of tracks in Fig 1A vs 1B). Thus, results suggesting overall decline in densities are conservative as our observational detection should have been improved in later years. Also, this technique allowed us to evaluate population trends at a hectare scale. More resolved techniques such as photo mosaics provide a much more precise assessment technique, but are still only applicable at meso-scales (hundresd of m2; Lirman et al. 2007)).

The substantial loss of *A. palmata* thicket area is a particularly concerning result. *Acropora* thickets are understood to have been the typical configuration on Caribbean reefs prior to the drastic decline of these species starting in the early 1980's (Goreau 1959; Jaap 1984) and are functionally important in terms of providing structural habitat both for other reef inhabitants and to facilitate fragment retention (i.e., successful asexual reproduction) for the coral itself. This importance is reflected in the fact that area of thickets (not just population abundance) has been defined as a key criterion for determining the recovery of these species under the US Endangered Species Act (NMFS 2015). The loss of *A. palmata* thicket area thus represents a trend opposing species recovery. The density of all *A. palmata* colonies also shows negative trends at most sites, both before and during the acute thermal bleaching event (Table 1). These alarming results emphasize the need for continued enhancement effort and development of approaches to more effectively convert *Acropora* spp. outplants into thickets.

Overall, population enhancement is associated with reef-scale positive trends in *Acropora cervicornis* in the Florida Keys. Unfortunately, this effect can be overpowered by massive thermal stress events such as was experienced in this region in 2014-15. These results point to the necessity of ongoing population enhancement efforts to foster species recovery (as mandated by the Endangered Species Act) but also to the insufficiency of current strategies in a rapidly warming ocean where future climatologies are unlikely to resemble those of the recent past (van Hooidonk et al. 2013). The identification of thermal resistance traits in corals and their mechanisms is crucial in order to devise additional assistive strategies to enhance the thermal resilience of threatened corals.

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Figure Legends:

Fig 1: Component maps and spatial analyses are illustrated for a single site, Grecian Rocks; a similar sequence of maps was constructed for each site and temporal comparison. Observed search tracks and waypoint features mapped for each census year (2006 points as stars, 2014 points as asterisks, 2015 points as triangles) are given in A)-C) with *A. palmata* colony waypoints depicted in yellow, *A. cervicornis* colonies in purple, and *A. palmata* thicktet outline points in orange. D-E) Merged maps for two temporal comparison showing the common observed area (determined by GIS intersect of the polygons determined by the search tracks for each year) for both years and the overlayed colony distribution observed in both years.

Fig 2: Area (m^2) of *A.palmata* thickets (i.e. high density aggregations for which mapping individual colonies was deemed infeasible) at four sites over time. Horseshoe was surveyed in both 2005 and 2007 so the point for this time period is a mean of these two. Thickets dropping to zero area likely still contained remnant colonies, but at lower densities such that individual colonies could be mapped (see text for details on methods).

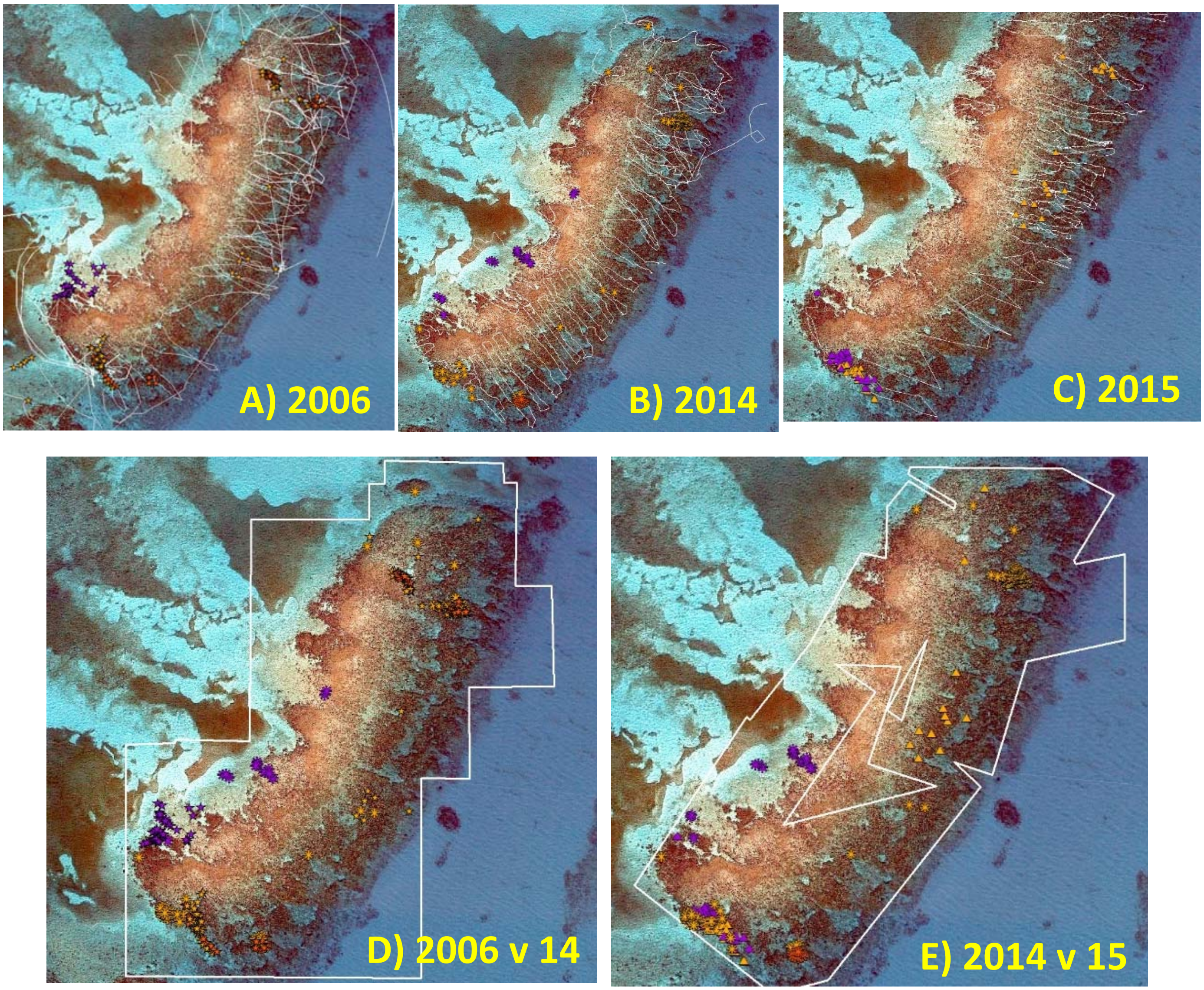
Fig 3: Proportional change in colony density (mean plus 1 SE; n=9 sites) for *Acropora cervicornis* (A) and *Acropora palmata* (B) during two time intervals. Right y-axis shows the cumulative number of fragments of each species outplanted to these sites during the same intervals. Note the differences in axis scales.

Fig 4: Scatterplot showing linear regressions for change in colony density relative to the cumulative number of outplants for A) *Acropora cervicornis* (full interval of observation, n=14 sites) and B) *Acropora palmata*. Population enhancement has only occurred for *A.palmata* since 2014, so B) shows proportional change in density for this species from 2014-2015 at n=9 sites (regression is not significant).

Figure 1(on next page)

Illustration of survey and spatial analysis

Component maps and spatial analyses are illustrated for a single site, Grecian Rocks; a similar sequence of maps was constructed for each site and temporal comparison. Observed search tracks and waypoint features mapped for each census year (2006 points as stars, 2014 points as asterisks, 2015 points as triangles) are given in A)-C) with *A. palmata* colony waypoints depicted in yellow, *A. cervicornis* colonies in purple, and *A. palmata* thicktet outline points in orange. D-E) Merged maps for two temporal comparison showing the common observed area (determined by GIS intersect of the polygons determined by the search tracks for each year) for both years and the overlayed colony distribution observed in both years.

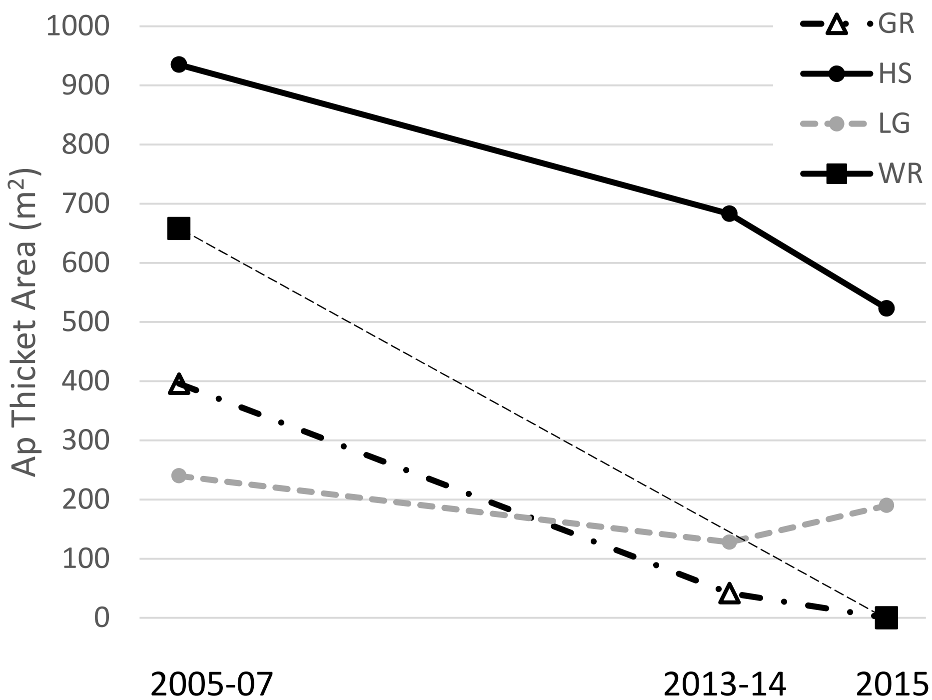


A) 2006
B) 2014
C) 2015
D) 2006 v 14
E) 2014 v 15

Figure 2(on next page)

Acropora palmata thickets

Area (m^2) of *A.palmata* thickets (i.e. high density aggregations for which mapping individual colonies was deemed infeasible) at four sites over time. Horseshoe was surveyed in both 2005 and 2007 so the point for this time period is a mean of these two. Thickets dropping to zero area likely still contained remnant colonies, but at lower densities such that individual colonies could be mapped (see text for details on methods).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1000
900
800
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600
500
400
300
200
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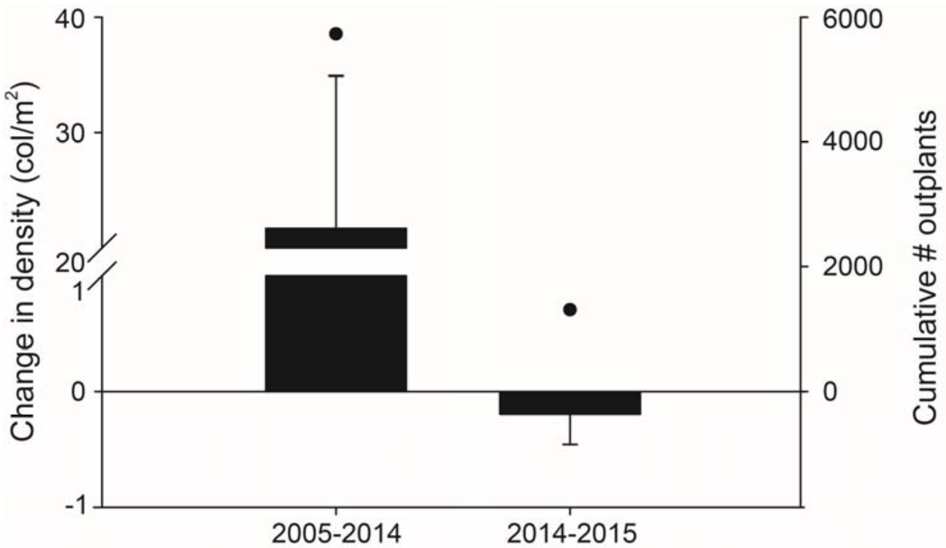
Ap Thicket Area (m²)
2005-07
2013-14
2015

Figure 3(on next page)

Acropora spp. change in density

A) *A.cervicornis*



B) *A.palmata*

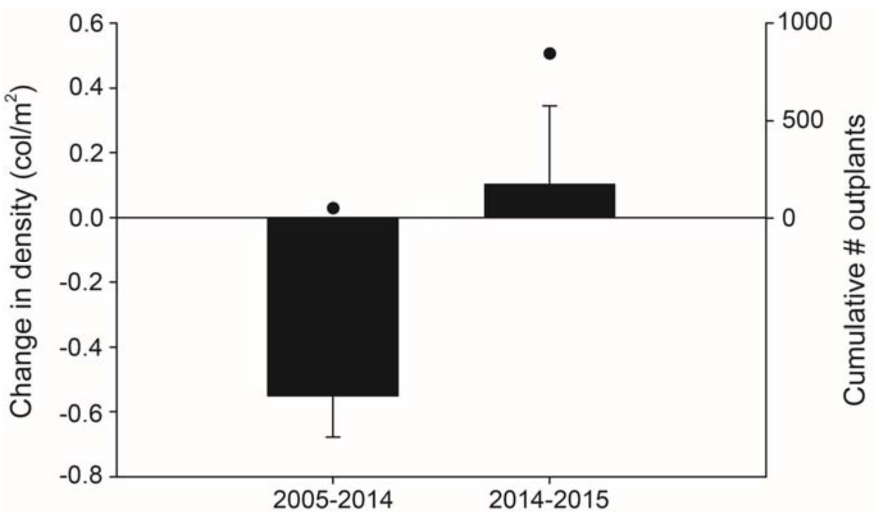


Figure 4
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Acropora spp change in colony density with population enhancement

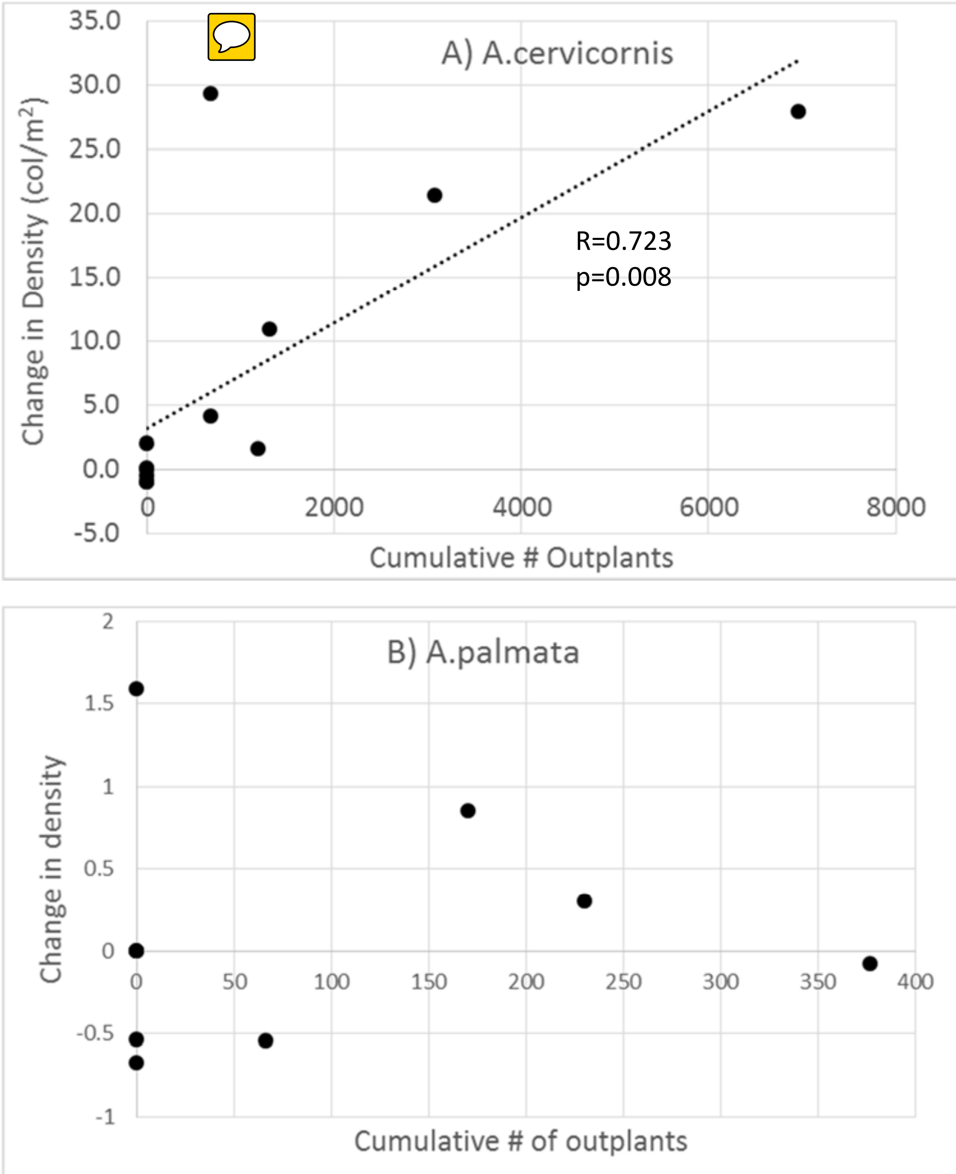
A) A.cervicornis
Change in Density (col/m2)
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
-5.0
0
2000
4000
6000
8000
Cumulative # Outplants
R=0.723
p=0.008
B) A.palmata
Change in density
2
1.5
1
0.5
0
-0.5
-1
0
50
100
150
200
250
300
350
400
Cumulative # of outplants

Table 1(on next page)

Long-term and short-term *Acropora* spp. changes at sites in the upper Florida Keys.

Table 1: Summary of congruent observed areas, colony densities, and number of outplants for both species over A) long term interval prior to 2014 thermal bleaching event and B) over the 2014-2015 bleaching event, at sites in the upper Florida Keys. Change in density is represented as a proportion of the initial density. Information on numbers of outplants provided by Coral Restoration Foundation, the only organization performing large-scale population enhancement in this region. CF=Carysfort, FR=French, ML=Molasses, NDR= North Dry Rocks, WBDR1/2= White Bank Dry Rocks north/south, LG= Little Grecian, GR = Grecian Rocks, NNDR = North North Dry Rocks, SI= Sand Island.

A)			*A. cervicornis*						*A. palmata*					
Reef	Years	Congr Area (ha)	#Ac-Early	AcDens -Early	#Ac-Late	AcDens-Late	**Change AcDens**	# Ac Outpl	#Ap-Early	ApDens-Early	#Ap-Late	ApDense -Late	**Change ApDens**	# Ap Outpl
CF	05 & 14	1.6	8	4.9	9	5.6	**0.1**	370	55	34.0	0	0.0	**-1.0**	0
FR	07 & 14	8.0	8	1.0	41	5.1	**4.1**	682	185	23.2	63	7.9	**-0.7**	0
ML	06 & 14	15.5	12	0.8	1331	85.8	**109.9**	3071	239	15.4	89	5.7	**-0.6**	0
NDR	06 & 14	3.9	109	28.3	3	0.8	**-1.0**	300	74	19.2	27	7.0	**-0.6**	50
WB DR 2	06 & 14	6.4	10	1.6	526	82.3	**51.6**	1307	0	0.0	0	0.0	**0.0**	0
WB DR 1	06 & 14	9.3	172	18.6	448	48.4	**1.6**	0	6	0.6	0	0.0	**-1.0**	0
LG	06 & 13	2.1	1	0.5	8	3.8	**7.0**	0	320	153.8	270	129.8	**-0.2**	0
GR	06 & 14	14.1	42	3.0	39	2.8	**-0.1**	0	408	29.0	276	19.6	**-0.3**	0

B)			*A.cervicornis*						*A. palmata*					
Reef	Years	Congr Area (ha)	#Ac-Early	Ac Dens Early	#Ac-Late	Ac Dens Late	**Change AcDens**	#Ac Outpl	#Ap-Early	Ap Dens Early	#Ap-Late	ApDense Late	**Change ApDens**	#Ap Outpl
CF	14 & 15	9.4	0	0.0	0	0.0	**0.0**	815.0	26	2.8	12	1.3	**-0.5**	66
FR	14 & 15	7.3	40	5.5	102	13.9	**1.6**	0.0	63	8.6	82	11.2	**0.3**	230
ML	14 & 15	13.5	1260	93.2	269	19.9	**-0.8**	915.0	89	6.6	82	6.1	**-0.1**	377
NDR	14 & 15	3.1	109	34.7	79	25.2	**-0.3**	388.0	74	23.6	137	43.6	**0.9**	170
WB DR2	14 & 15	5.6	526	93.4	194	34.5	**-0.6**	0.0	0	0.0	0	0.0	**0**	0
WB DR1	14 & 15	6.2	446	71.7	84	13.5	**-0.8**	0.0	0	0.0	0	0.0	**0**	0
NN DR	13 & 15	2.6	8	3.1	0	0.0	**-1.0**	0.0	34	13.0	88	33.7	**1.6**	0
LG	13 & 15	3.5	18	5.1	15	4.3	**-0.2**	0.0	60	17.1	28	8.0	**-0.5**	0
SI	14 & 15	3.5	0	0.0	0	0.0	**0.0**	0.0	106	30.7	35	10.1	**-0.7**	0