

Session 6

Coral conservation in times of change: letting nature pick the winners

Session chairs:

Madhavi A Colton, mcolton@coral.org

Michael S. Webster, mwebster@coral.org

Malin L. Pinsky, malin.pinsky@rugters.edu

Lunz KS, Shea C, Ames KW, Neely K, Goergen E, Williams D, Gilliam DS, Whittle A (2016)
Acropora palmata's last stand in Florida? Proceedings of the 13th International Coral Reef Symposium,
Honolulu: 2-22

Acropora palmata's last stand in Florida?

K.S. Lunz, C. Shea, K.W. Ames, K. Neely, E. Goergen, D. Williams, D.S. Gilliam, A. Whittle

Abstract Based on five years of demographic monitoring of wild *Acropora palmata* along the Florida Reef Tract, the strongest predictors of monthly colony survival were factors related to season, year, region, and initial skeletal area. While colony survival was generally lowest in Biscayne National Park and the Lower Florida Keys, colonies throughout the Florida Reef Tract were greatly affected (241 of the 514 original colonies were lost) by presumed temperature anomaly-induced stress occurring during summer 2014 and lasting through the onset of El Niño during winter 2014/2015. In addition to spatial and temporal differences, colony survival also was strongly and positively related to skeletal area, indicating that larger colonies were more likely, on average, to survive until the end of the five year study period than smaller colonies. These results suggest a higher survival chance for large, nursery-reared outplants relocated to region-specific areas with current conditions that appear conducive to survival and high abundance of colonies (Upper and Middle Keys).

Keywords: *Acropora palmata*, Florida reef tract, survival, size-specific mortality, seasonal effects

K. S. Lunz, C. Shea, K. W. Ames, K. Neely
Fish and Wildlife Research Institute, Fish and Wildlife Conservation Commission, 100 8th Ave SE, Saint Petersburg, FL 33705

D. Williams
Cooperative Institute for Marine and Atmospheric Studies, University of Miami, 4600 Rickenbacker Cswy, Miami, FL 33149, USA

E. Goergen
Halmos College of Natural Sciences and Oceanography, Nova Southeastern University, 8000 North Ocean Drive, Dania Beach, FL 33004

Communicating author: K.S. Lunz, (kate.lunz@myfwc.com)

Introduction

The combination of a broad, shallow continental shelf and the warm Gulf Stream water provides a unique suite of benthic habitats that support Florida's coral reef ecosystems (Andrews et al. 2005). All

regions are subject to unique environmental conditions and, subsequently, varying degrees of coral cover and species composition (Andrews et al. 2005; Walker 2012). Numerous stressors affect coral health throughout Florida, including, but not limited to: bleaching, diseases, water pollution, predation, physical impacts, tropical storms, winter cold fronts, and anthropogenic impacts (Andrews et al. 2005). While all of the reef-building stony coral species along the Florida Keys have exhibited significant overall declines in cover in recent decades at shallow fore-reefs (Ruzicka et al. 2013), the most notable decline has occurred in cover of the once-dominant acroporid species (*Acropora cervicornis*, *Acropora palmata*) (Jaap et al. 1988; Porter and Meier 1992; Bythell and Sheppard 1993; Miller et al. 2002). Elkhorn and staghorn corals (*A. palmata* and *A. cervicornis*) were listed as threatened under the Endangered Species Act in 2006 (National Marine Fisheries Service 2006) and, in 2008, were listed as critically endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Aronson et al. 2008a, 2008b).

Acropora palmata is characterized by parallel, oblique, very thick tapered branches, thus its common name, Elk Horn coral (Veron 2000). *A. palmata* and *A. cervicornis* have the fastest growth and calcification rates of any species in the Caribbean (Dullo 2005). Historically, *A. palmata* was the major reef-builder in the shallow fore-reef, high wave action zones of the Florida Reef Tract (Dustan 1985; Shinn et al. 1989; Shinn 2004) and the extensive three-dimensional structure of *Acropora* thickets provided habitat for many reef fish (Gladfelter et al. 1978; Lirman 1999). The habitat of *A. palmata* has been so well defined that its distribution has been used to interpret both modern- and paleo-environments; for example, Hubbard (1989; 1997) used the occurrence and morphologies of *A. palmata* as an indicator of wave and storm prevalence on reefs. Because this species is adapted to high light intensities and, therefore, water depths typically less than 10 m, its fossil distribution has been widely used to interpret rates of sea level rise (Blanchon and Shaw 1995; Toscano and Lundberg 1998; Blanchon and Eisenhauer 2001; Toscano and Macintyre 2003; Brock et al. 2008; Gabriel et al. 2009; Blanchon 2010).

Here, we present demographic status and trends data for Florida's wild *A. palmata* population occurring across the Florida Reef Tract from 2010-2015, including important implications for colony size and regional influence that could aid in future *A. palmata* restoration and outplant strategies. We modeled monthly survival of individual colonies as a function of various time, site, and colony-specific predictor variables that we hypothesized may influence the survival of coral colonies (further defined in Table 1). Our hypothesized positive-influence predictor variables included initial skeletal area, light488

(percent of photosynthetically available radiation, $\lambda = 488$ nm, reaching the benthos), and the seasons winter and spring. Our hypothesized negative-influence predictor variables included distance from shore, light_{488}^2 (a quadratic term), and the summer season. Predictor variables expected to have a variable influence on colony survival included habitat type and region.

Materials and methods

Study Sites

Sites were chosen within six regions along the Florida Reef Tract based on the spatial distribution of the existing population (from north to south): the Southeast Florida or Southeast Florida Coral Reef Initiative region (SEFCRI, comprising Miami-Dade, Broward, and Palm Beach counties), Biscayne National Park, Upper Keys, Middle Key, Lower Keys and Dry Tortugas National Park. The regional distinctions were developed based on management entity boundaries (State of Florida waters, and federal waters managed by either the National Park Service or the National Marine Fisheries Service) and regional boundaries commonly employed by reef monitoring programs, such as the Coral Reef Evaluation and Monitoring Program (Ruzicka et al. 2013). Within the SEFCRI region, nine sites containing single colonies of *A. palmata* were established for monitoring to ensure spatial coverage across the entire Florida Reef Tract. At a total of 52 sites, one to five 7 m radial circular plots were established as site-level replicates following the protocol of Williams et al. (2006) (Fig. 1).

Field Methods

Within each 7 m radial circular plot, all *A. palmata* colonies were mapped, measured, and photographed. During the initial setup and subsequent annual mapping surveys, colony density, as well as skeletal area (a function of colony length, width, and height) and percent live tissue and evidence of stress for each colony were measured. All fate-tracked colonies had live tissue present during the initial survey event (i.e., when they entered the study), but the amount of live tissue varied widely among colonies (mean = 31%; range = 0.1% to 100%). For plots containing more than 18 colonies, 12 colonies were randomly selected and tagged for long-term tracking of individuals. If a plot contained less than 18 colonies, all colonies were fate-tracked. These fate-tracked colonies were visited three times annually (with a few exceptions due to weather) between summer 2010 and winter 2014/2015, resulting in a study period

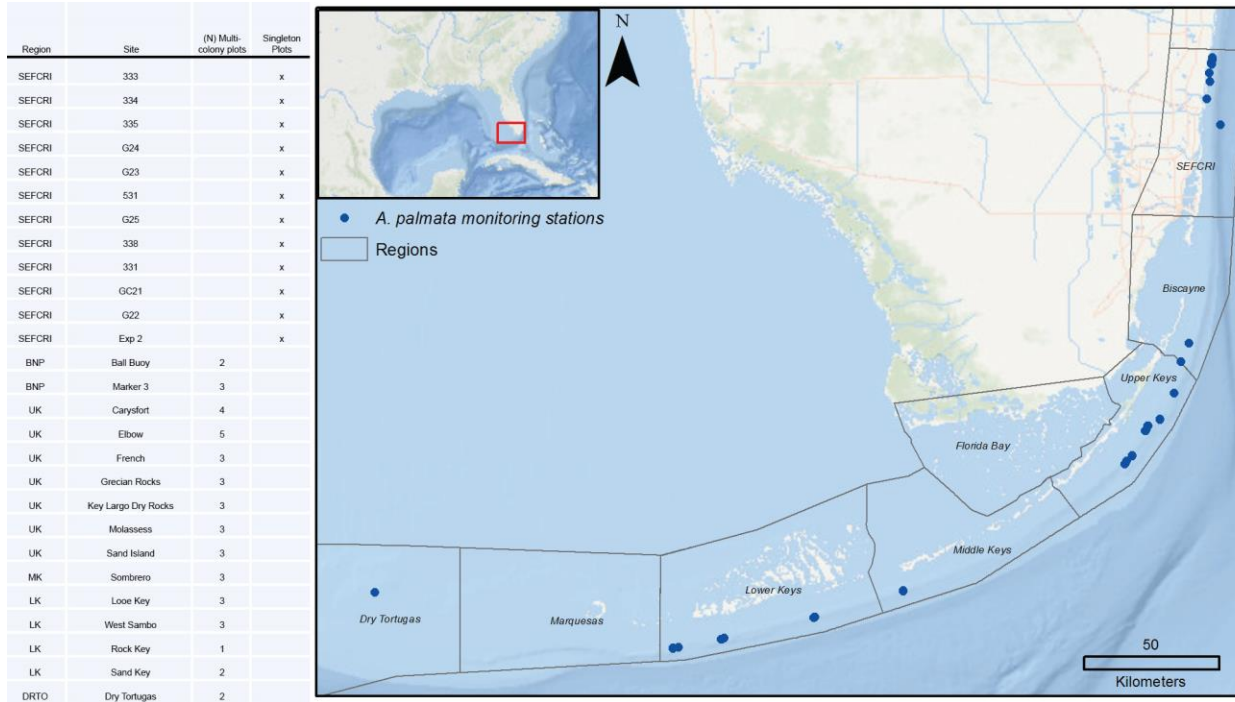


Fig. 1 *Acropora palmata* monitoring stations. A total of 52 sites were monitored three times annually from 2010 to 2015, with sites distributed among the six regions of the Florida Reef Tract.

lasting 56 months. During each survey, the fate-tracked colonies were measured for percent of the colony covered with live coral tissue and evidence of stress factors including bleaching, disease and corallivorous snails, following the methods of Williams et al. (2006). Although percent live tissue and the presence of bleaching, disease, and corallivorous snails were recorded in the surveys, they were omitted from the models used in the present study, and are part of ongoing research quantifying the effect of these stressors on *A. palmata*.

Analyses

Modeling of Monthly Colony Survival

We used a Bayesian hierarchical survival model (Royle and Dorazio 2008; Schmidt et al. 2010; hereafter, survival model) to estimate monthly survival of fate-tracked *A. palmata* colonies at locations throughout the Florida Keys. A total of 514 individual colonies were monitored at 52 sites from the SEFCRI region south to the Dry Tortugas from August 2010 – March 2015, and each colony had its own unique observation interval within the 56-month study period. All monthly periods that occurred prior to the entry of a colony into the study (i.e., before which there was no data) or following the death

of a colony (i.e., after which there was no data) were left and right censored (i.e., omitted from the analysis), respectively. We modeled the observed data for each colony as a Bernoulli random variable, denoted by $y_{it} \sim \text{Bernoulli}(\Phi_{it})$, where y_{it} represented the status (alive = 1; dead = 0) of colony i during month t , and Φ_{it} represented the probability that colony i was alive at time t , given the colony was alive at time $t-1$. Under the Bayesian modeling framework, the status of coral colonies (alive or dead) within the period of observation (i.e., following a colony's first month of observation and up to the final month of observation) could be predicted by the model for each coral colony during months when a colony was not observed in the field. For example, a colony may have been observed dead during the 20th month of observation, but because several months may have passed since the colony was last observed alive, there was uncertainty surrounding when the colony death actually occurred. The ability to predict the status of colonies during months when no surveys occurred helped to reduce potential biases associated with this uncertainty (Royle and Dorazio 2008).

We used a logit link function to model monthly colony survival, Φ_{it} , as a function of various time, site, and colony-specific predictor variables that we hypothesized may influence the survival of coral colonies (Table 1). As skeletal area was measured for each colony during the initial survey event, the skeletal area predictor variable in this study represented the skeletal area of colonies at the time of the first survey (i.e., where they started out). Although percent live tissue was measured during each survey event, it was not included as a covariate in the survival model (described below) for the following reasons: (1) its value was highly temporally variable, resulting in uncertainty surrounding its value during months when sampling did not occur; and (2) interpolation of percent live tissue during periods of non-observation was beyond the scope of our modeling framework. Hence, we opted for the inclusion of skeletal area, which was relatively stable for each colony over the course of the study, as the sole colony-specific covariate in the survival model.

The predictor variable habitat type was based on the Unified Florida Reef Tract Map (Baumstark 2013). Distance from shore was calculated for each site, by measuring the Euclidian distance (to the nearest km) to the nearest shoreline. In addition to distance from shore, we assessed the predominant light conditions at each of the 52 sites using MODIS/Aqua satellite-derived values of the diffuse attenuation coefficient (K_d) at 1 km² spatial resolution, which were obtained from University of South Florida's Optical Oceanography Laboratory. The Optical Oceanography Laboratory used an improved algorithm to obtain K_d values over the optically shallow water of the Florida Keys (Barnes et al. 2013). We used the climatological coverage $K_d(488)$, or photosynthetically available radiation (PAR, $\lambda = 488$

nm) reaching the benthos, as a predictor variable (light488). We also included a light488 quadratic term (light488²) to assess whether or not there was an optimal light488 level with respect to colony survival. Extreme low and high light488 levels are detrimental to colony survival, whereas intermediate levels are associated with higher colony survival (Lesser 2011).

To facilitate model fitting, all continuous covariates were standardized to have mean of 0 and standard deviation of 1, and uninformative normal prior distributions were used for all model parameters. The global (all predictors) model was fit in OpenBUGS software (Lunn et al. 2009) using 100,000 MCMC iterations and 50,000 burn-in, and MCMC convergence was assessed using the Gelman-Rubin diagnostic (Gelman et al. 2004). We based all inferences on posterior means, 95% credible intervals (CIs), and odds ratios (OR) from the global model, with parameters considered important if their CIs did not overlap zero (King et al. 2016). Three additional predictor variables, the presence of bleaching, disease, and corallivorous snails, were included in our initial modeling efforts; however, they were omitted from the model because we suspected they could result in misleading inferences as it was not possible to observe their values during months when surveys were not conducted.

Results

Overall, 241 of 514 colonies died during the course of this study along the entire study area. Bayesian hierarchical survival modeling results suggest that colony survival varied substantially in relation to initial skeletal area, regions, seasons, and years (Table 2; Figs. 2-7). Specifically, survival generally depended on initial skeletal area, region, and season, with lower survival probabilities associated with the regions Biscayne National Park and the Lower Keys, all summer seasons (summer 2010-2013, summer 2014), and winter 2014/2015.

Parameter estimates from the global survival model indicated that monthly colony survival was strongly and positively related to initial colony size, represented in this study by initial skeletal area (Table 2; Figs. 2-4). Odds ratios indicated that for every 1 SD (0.76 m²) increase in initial skeletal area (mean = 0.47 m², range = 0.0002-5.70 m²), coral colonies were 2.07 times more likely to survive a monthly

Table 1 Predictor variables included in the hierarchical Bayesian survival model relating colony, site, and time-specific factors to monthly survival of coral colonies at locations throughout the Florida Reef Tract.

Predictor Variable	Description	Hypothesis/Rationale	Supporting References
<i>Colony-specific</i>			
	The skeletal area (m ²) of each colony: $((L+W+H)/3)^2$.	Skeletal area has a strong positive correlation to age. Larger/older colonies are more resilient to stressors and less likely to suffer complete mortality than smaller/younger colonies.	Hughes (1984), Hughes (1987), Raymundo and Maypa (2004)
<i>Site-specific</i>			
Light488 and Light488 ²	Percent of 488 wavelength light reaching the benthos and represents the amount of photosynthetically available radiation (PAR), on average, to each colony based on its location. Light488 ² is a quadratic term.	Light488 has a strong positive correlation with survival. More light availability is beneficial to this species. Light488 ² has a possibly moderate, negative effect on survival, but likely varies among colonies and the presence of other risk factors. Generally, too little or too high is detrimental, but moderate levels are good.	Wells (1957), Done (1983), Fenner (1988), Hubbard (1997), Yentsch et al. (2002), Mass et al. (2010), Ames (2016)
Distance to shore	Distance (km) to nearest shore.	Distance from shore is negatively related to monthly survival along the Florida Reef Tract because colonies closer to shore may be better adapted to higher stress regimes.	Lirman and Fong (2007), Manzello et al. (2012), Ruzicka et al. (2013)
Habitat Type	Binary variable: 1 = yes; 0 = no. Spur and groove served as the baseline, so not included in the model. The remaining possibilities were: Pavement and a combined grouping of Aggregate/Ridge/Reef-Rubble.	Monthly survival varies among reef types because of differences in physical habitat conditions. Spur/groove is the preferred habitat for this species.	Shinn et al. (1989), Baumstark (2013), Wirt et al. (2015)
Region	Binary variable: 1 = yes; 0 = no; Upper Keys served as the baseline, so not included in the model. The remaining possibilities were: Dry Tortugas, Lower Keys, Middle Keys, Biscayne, and SEFCRI.	Monthly survival varies spatially among the 6 distinct geographic regions included in this study.	Andrews (2005), Walker (2012)
<i>Time-specific</i>			
Spring 2011-2014	Binary variable: 1 = spring (April-July); served as the baseline, so not included in the model.	Positively correlated with survival. Corals have recovered from summer stress and are maintaining; survival generally highest at this time.	Fitt et al. (2000)
Summer 2010-2013	Binary variable: 1 = summer (August-October); 0 = spring or winter.	Negatively correlated with survival. High risk of mortality: colonies more prone	Fitt et al. (2000)

		to bleaching, high temperatures, and disease.	
Winter 2010/11 - 2013/2014	Binary variable: 1 = winter; 0 = spring or summer.	Positively correlated with survival. Period of recovery and growth; survival similar to spring, but possibly slightly lower due to cold temperatures, lags from summer stress.	Fitt et al. (2000)
Summer 2014	Binary variable: 1 = summer 2014 (August-October); 0 = all other time periods.	Negatively correlated with survival. Exceptionally poor survival for all coral species was documented during this time period along the Florida Reef Tract (FWC, FRRP).	Fitt et al. (2000), Manzello (2015), FWC (2016), FRRP (Summer 2015)
Winter 2014/2015	Binary variable: 1 = winter 2015 (November-March); 0 = all other time periods.	Negatively correlated with survival. Exceptionally poor survival during this time period due to onset of El Niño conditions.	Fitt et al. (2000)

interval. Parameter estimates also indicated that coral colonies in Biscayne National Park and the Lower Keys were 1.82 (1/0.549) and 2.35 (1/0.426) times less likely, respectively, to survive a monthly interval relative to colonies in the SEFCRI, Upper Keys, Middle Keys, and Dry Tortugas Regions (Table 2; Figs. 2-4). Modeling results also revealed that monthly colony survival was generally lower during summer in all years relative to the baseline spring season, and substantially lower in summer 2014 (Table 2; Figs. 2-4). Odds ratios indicated that colonies were 2.51 times (1/0.398) less likely to survive during normal summer months (2010-2013) relative to spring, whereas colonies were 7.25 times (1/0.138) less likely to survive summer months during 2014 (Table 2). Although colony survival was generally similar between winter and spring during most years, colonies were, on average 11.97 (1/0.084) times less likely to survive in winter 2014/2015 relative to the baseline spring season (Table 2). Lastly, modeling results also indicated that monthly colony survival was weakly and negatively related to light488 (defined in Table 1), with survival 1.57 times (1/0.639) less likely for every 1 SD (11.6%) increase in light488 (mean = 70%; range =36-88%). Parameter estimates for the remaining predictor variables light488², pavement, aggregate/ridge/reef-rubble, and distance to shore were considered imprecise as the 95% credible intervals contained zero.

Table 2 Parameter estimates (Mean; logit scale), standard deviations (SD), 95% credible intervals (CI), and odds ratios (OR) from the global Bayesian hierarchical survival model relating monthly coral colony survival to colony-, site-, and time-specific factors. Parameters strongly influencing survival are bolded.

Parameter	Mean	SD	95 % CI		OR
			Lower	Upper	
Intercept	5.456	0.301	4.908	6.118	
Skeletal Area	0.729	0.115	0.511	0.963	2.073
Distance to Shore	-0.154	0.183	-0.515	0.204	0.857
Light 488	-0.448	0.088	-0.623	-0.275	0.639
Light 488 ²	-0.071	0.051	-0.170	0.034	0.932
Pavement	0.011	0.219	-0.425	0.433	1.011
Aggregate/Ridge/Reef-Rubble	0.041	0.183	-0.322	0.408	1.042
SEFCRI	0.477	0.997	-1.380	2.550	1.611
Biscayne National Park	-0.599	0.239	-1.078	-0.135	0.549
Lower Keys	-0.854	0.194	-1.247	-0.481	0.426
Middle Keys	-0.338	0.569	-1.424	0.905	0.713
Dry Tortugas	-0.429	0.794	-2.029	1.115	0.651
Summer 2010-2013	-0.921	0.324	-1.562	-0.268	0.398
Summer 2014	-1.981	0.317	-2.625	-1.362	0.138
Winter 2010/11-2013/14	0.230	0.347	-0.462	0.921	1.259
Winter 2014/2015	-2.482	0.263	-3.023	-1.980	0.084

Estimation of seasonal colony survival

Using parameter estimates from the global survival model, we estimated season-specific survival probabilities as derived parameters for three colony size (skeletal area) categories (small: 0.0002 m², average: 0.47 m², and large: 5.70 m²) in each of three distinct regional groups: (1) each size category and region, the seasonal survival probabilities represented the expected cumulative probability of survival during summer (August-October), winter (November-March), and spring (April – July). For example, summer survival was calculated as the product of predicted monthly survival probabilities during August, September, and October (Table 1).

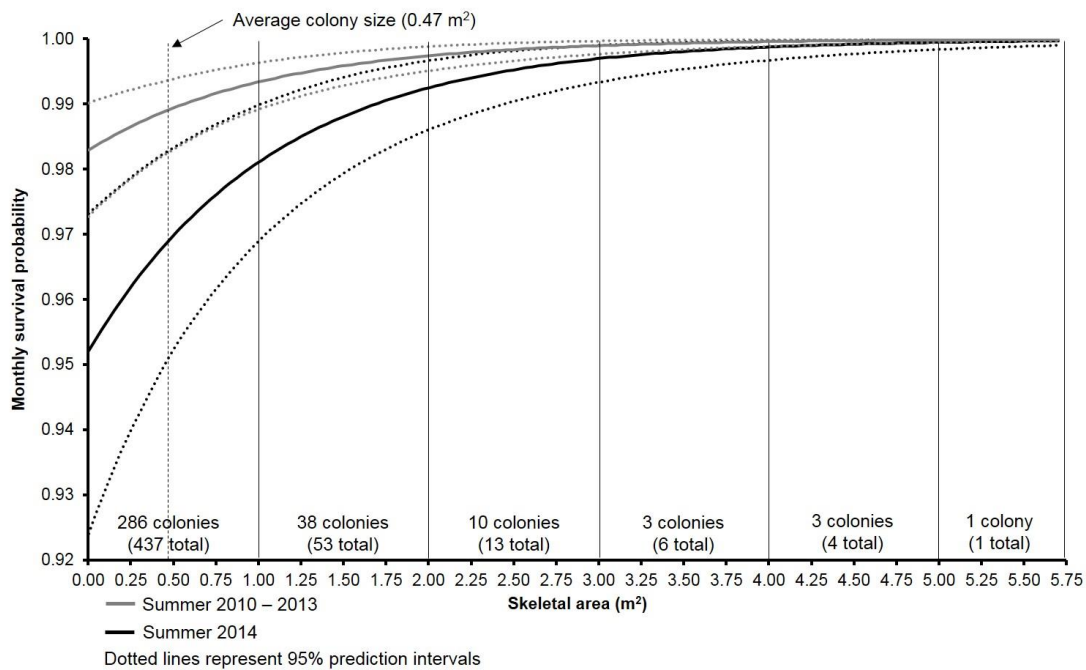


Fig. 2 The relationship between colony size and monthly (not cumulative) survival during relatively mild (2010-2013) and temperature anomaly (2014) summers for sites within the Dry Tortugas, Middle Keys, Upper Keys, and SEFCRI regions. A count of the number of colonies in each 1.0 m² bin is included to demonstrate how many colonies in these regions fell into each of these general size categories. The total number of colonies in each size category across all regions are listed in parentheses. The upper and lower limits on the x-axis are 0.0002 and 5.70 m², respectively.

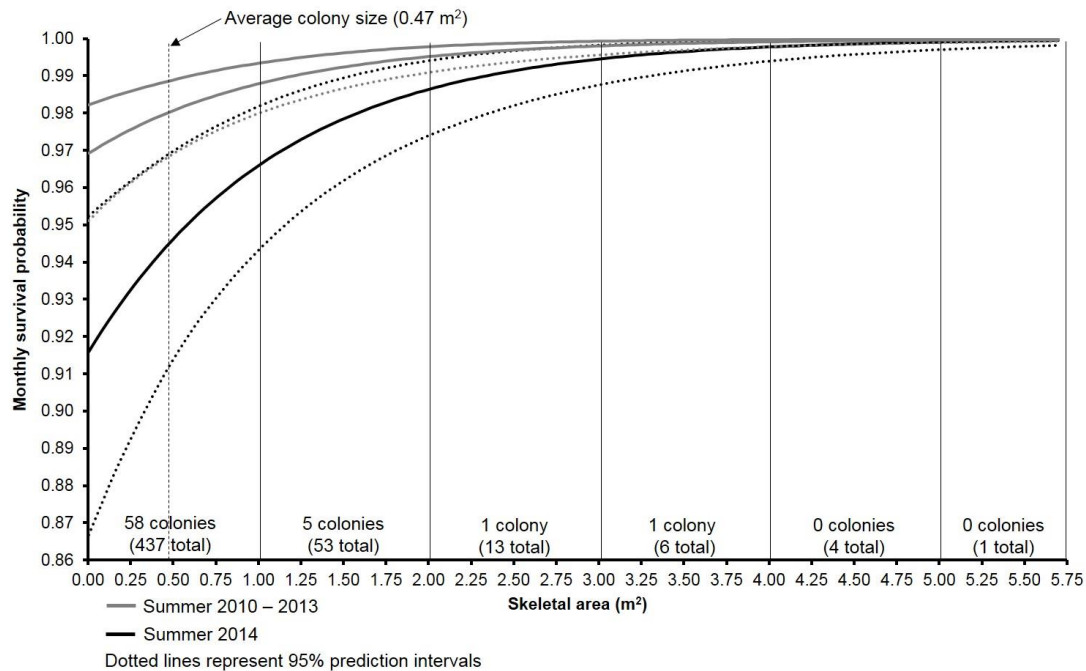


Fig. 3. The relationship between colony size and monthly (not cumulative) survival during relatively mild (2010-2013) and temperature anomaly (2014) summers within the Biscayne National Park region. A count of the number of colonies in each 1.0 m² bin is included to demonstrate how many colonies in the region fell into each of these general size categories. The total number of colonies in each size category across all regions are listed in parentheses. The upper and lower limits on the x-axis are 0.0002 and 5.70 m², respectively.

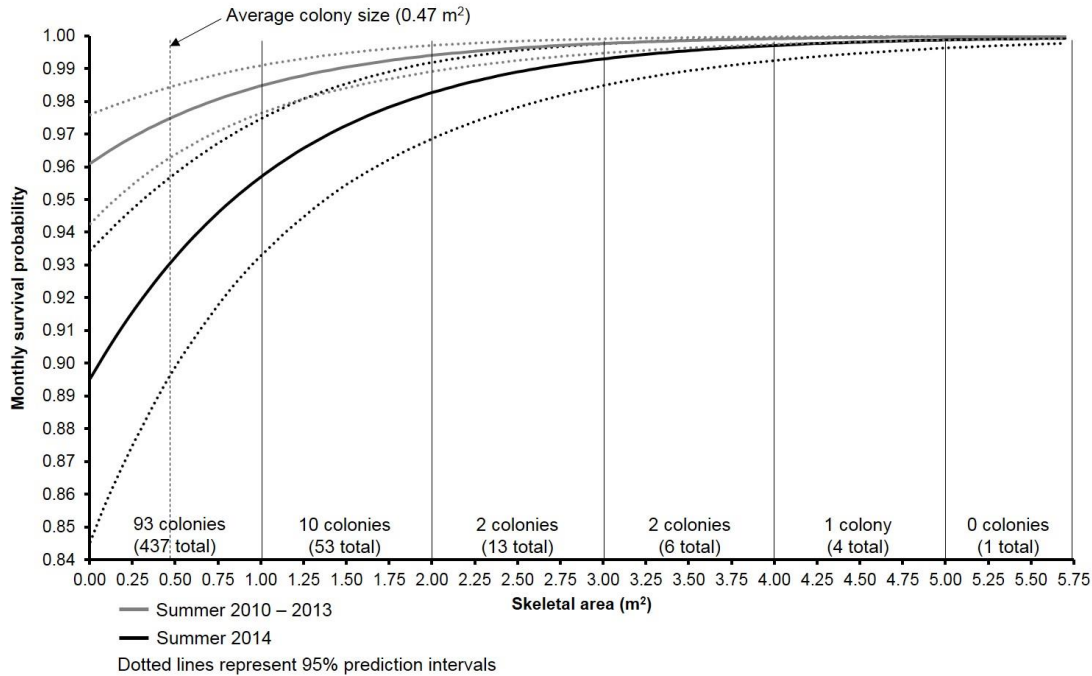


Fig. 4 The relationship between colony size and monthly (not cumulative) survival during relatively mild (2010–2013) and temperature anomaly (2014) summers within the Lower Keys. A count of the number of colonies in each 1.0 m² bin is included to demonstrate how many colonies in the region fell into each of these general size categories. The total number of colonies in each size category across all regions are listed in parentheses. The upper and lower limits on the x-axis are 0.0002 and 5.70 m², respectively.

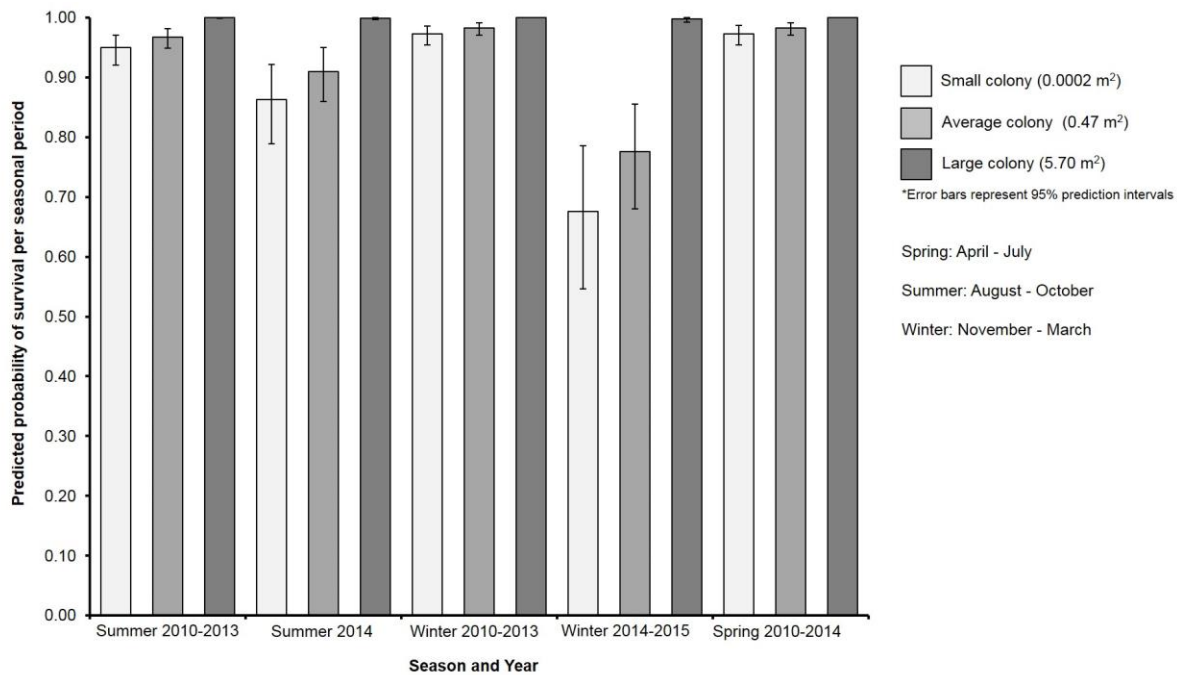


Fig 5 Estimated seasonal survival for small, average-sized, and large colonies in the Dry Tortugas, Middle Keys, Upper Keys, and SEFCRI regions. Seasonal survival estimates for each size class are based on parameter estimates from the global Bayesian hierarchical survival model. Error bars represent 95% confidence intervals.

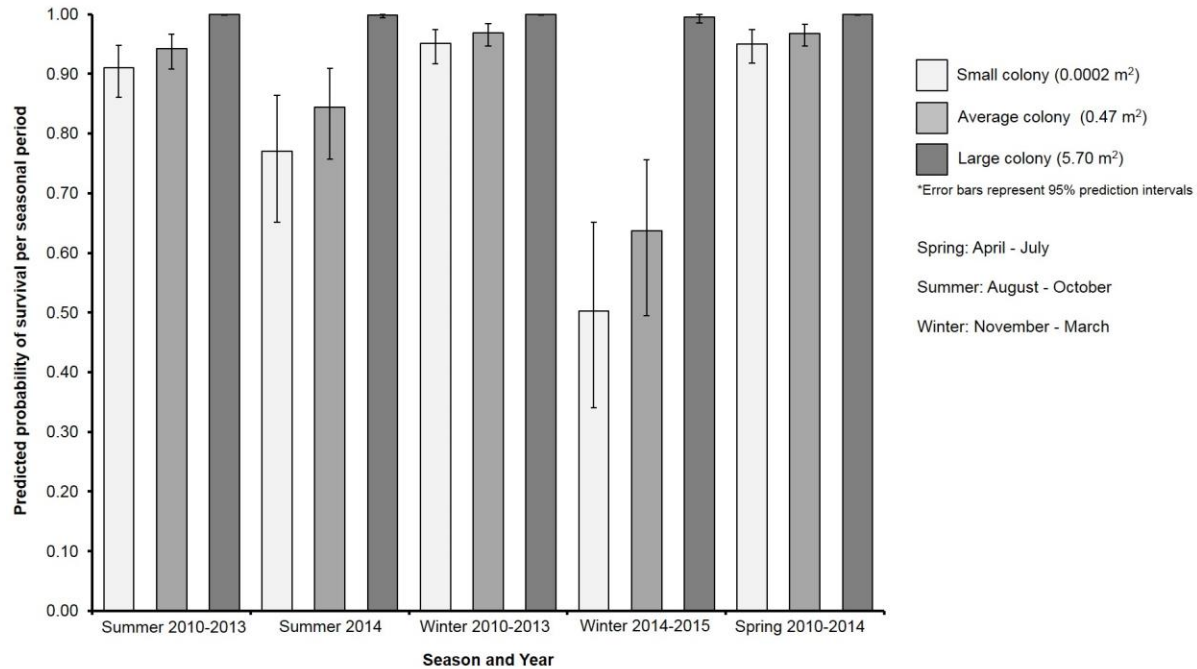


Fig. 6 Estimated seasonal survival for small, average-sized, and large colonies in the Biscayne National Park region. Seasonal survival estimates for each size class are based on parameter estimates from the global Bayesian hierarchical survival model. Error bars represent 95% confidence intervals.

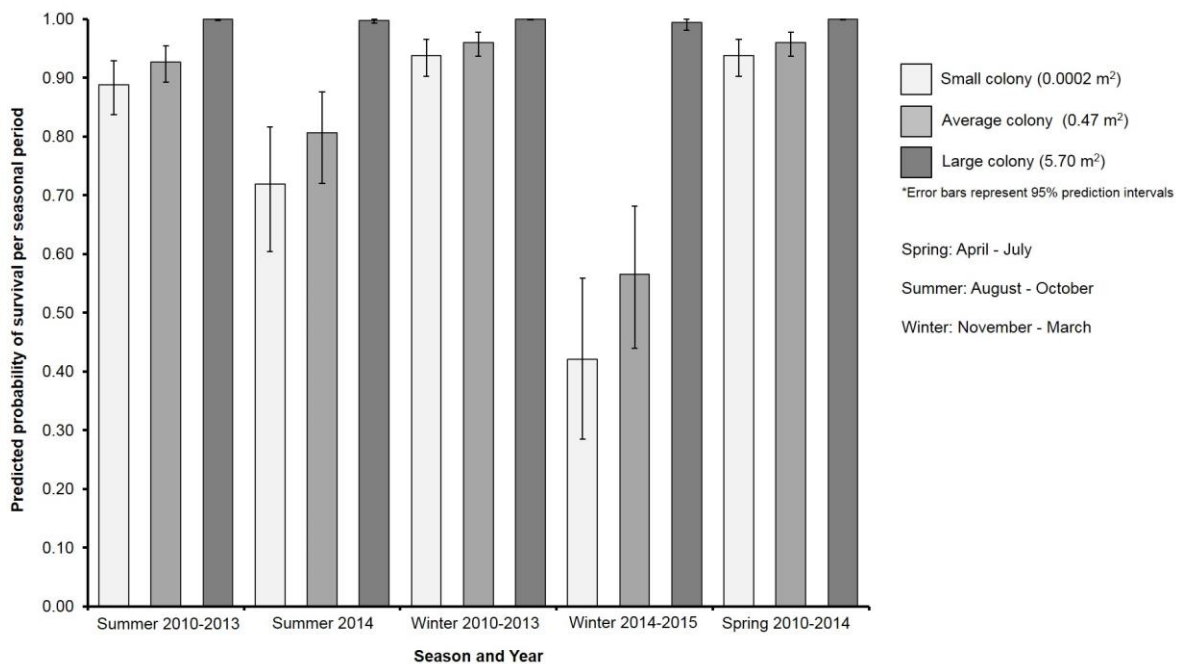


Fig. 7 Estimated seasonal survival for small, average-sized, and large colonies in the Lower Keys region. Seasonal survival estimates for each size class are based on parameter estimates from the global Bayesian hierarchical survival model. Error bars represent 95% confidence intervals.

Discussion

The main factors influencing *A. palmata* survival during the course of this project were season, year, region, and initial skeletal area. Corals fared better in the cooler winter and spring months of non-anomaly years across all regions; however, stressful conditions from summer 2014 and winter 2014/2015 rendered corals less likely to survive relative to the baseline spring season. Colonies within Biscayne National Park and the Lower Keys were overall less likely to survive, relative to colonies in all other regions. Additionally, monthly colony survival was strongly and positively related to initial skeletal area. We did not explore the relationship between percent live tissue and survival in this study, nor did we evaluate trends in asexual reproduction that were recorded in our annual mapping surveys; however, we will be incorporating these metrics into a revised model for a future manuscript.

Monthly survival was strongly and positively related to initial colony skeletal area. This finding is in general agreement with previous research which has shown that while whole colony mortality most strongly influences smaller size classes in coral populations (Bak and Meesters 1998), partial mortality is the dominant process affecting larger colonies (Hughes 1984). These general patterns are thought to arise because small colonies can be smothered or abraded by sediment, eaten or bulldozed by grazers and predators, and shaded or smothered by competitors (Hughes and Connell 1999). In contrast, large colonies are less susceptible to the stressors described above, but large colonies also tend to be chronically injured, which can expose bare skeleton and render them more susceptible to fouling or boring organisms (Hughes and Connell 1999). Thus, similar to other coral species, colony size is clearly an important determinant of colony survival for *A. palmata*.

Acropora palmata monthly colony survival varied among regions. Specifically, we found evidence that colony survival was lowest in the Lower Keys region and in Biscayne National Park, whereas monthly survival was similar among the remaining four regions, Upper Keys, Middle Keys, Dry Tortugas, and SEFCRI. Although we suspected that survival may vary among locations, we did not have any region-specific information (i.e., region-specific covariates) to inform why this pattern exists. Our finding of lower survival in the Lower Keys and Biscayne National Park could be attributed to a variety of factors that were not accounted for in our analysis, such as reductions in water quality, relatively higher average water temperatures that make bleaching and disease more likely, or aspects of local physical habitat that were not captured by our reef-type classifications. Additionally, filling gaps in our genetic and genotypic knowledge of *A. palmata* populations may shed light on regional differences in survival revealed by this study. For example, potentially high genetic diversity in the Upper Keys (e.g.,

the 12 genets identified at Sand Island) may be contributing to increased survival at some sites, as well as to the wide variability of survival in this region (Baums et al. 2005). Still, nine genets were identified at Western Sambo (Baums et al. 2005), a site in the Lower Keys that suffered catastrophic mortality during the present study. Regardless of the mechanisms, survival of *A. palmata* colonies appears to vary regionally within the Florida Reef Tract.

Acropora palmata colony survival varied seasonally, but the extent to which seasonal survival varied differed markedly among years. Our seasonal classifications represented three general periods during which coral colonies were exposed to distinct environmental conditions: spring (April – July) was assumed to be a period of limited stress during which coral colonies underwent growth and maintenance, summer (August – October) was assumed to be a period of increased stress during which colonies were more likely to experience higher temperature extremes and an elevated risk of bleaching and disease, and winter (November – March) was assumed to be a period of relatively low stress and recovery from higher stress conditions during the previous summer. We also suspected that seasonal survival varied among years, specifically during summer 2014 due to the onset of a thermal anomaly and in winter 2014/2015 due the onset of El Niño conditions. Our results indicated that seasonal survival was, on average, similar during winter and spring and generally lowest during summer. A notable exception to this general pattern was winter 2014/2015, when monthly survival was lower than any other season in the 56-month-long study period. Interestingly, the previous summer (summer 2014) exhibited a similarly low monthly survival rate. We suspect that the exceptionally low survival during summer 2014 was due to prolonged high temperatures that rendered colonies more prone to bleaching and disease, and the negative effects appear to have carried over into the following winter.

We hypothesized that colony survival would be higher in the presence of elevated levels of light488, which represented the amount of PAR in the water column. However, our modeling results indicated a negative relationship between colony survival and light488. This relationship may be due to multiple characteristics of this environmental layer. For example, the spatial resolution of the light488 layer was restricted to 1 km, which may not have accurately represented the site-specific light reaching the benthos. Additionally, the typically shallow environment required for *A. palmata* to thrive may result in a significant difference between light availability at the site and the overall average light availability of the 1 km pixel scale. Alternatively, the use of a light380 variable was considered as a predictor variable in the survival model, but this variable was found to be strongly and positively correlated with light488; hence, light380 was subsequently dropped from the model in favor of light488 to avoid multi-

collinearity. Because the light380 variable represents the potentially harmful light in the UV portion of the electromagnetic spectrum, it is possible that any positive effect of elevated light488 levels on colony survival may have been overwhelmed by the negative effect of elevated UV light levels. Interestingly, we also found no evidence for a strong quadratic effect of light488 (light488^2), which we included because we suspected that extreme (low and high) PAR levels would negatively influence colony survival. The lack of evidence for a quadratic effect strengthens our suspicion that a negative effect of light380 on colony survival could have overwhelmed any positive influence associated with greater amounts of PAR (light488) in the water column. Future studies related to light availability and colony survival may benefit from evaluating the influence of these parameters at finer spatial and temporal scales.

The habitat types evaluated in the present study do not appear to influence *A. palmata* colony survival. We expected that colonies inhabiting the most common reef habitat type, spur and groove, would have higher survival relative to pavement and aggregate/patch reef/ridge habitat types, as previous research have shown differential survival among habitat types for outplanted colonies (Smith and Hughes 1999). The lack of influence of habitat type in the present study may be related to multiple factors. One explanation is that our habitat classifications were too broad to capture ecologically or biologically important differences in physical habitat that would better explain differences in colony survival. Alternatively, it is possible that reef type may no longer be an important determinant of colony survival in the Florida Reef Tract. For example, although *A. palmata* colonies may have historically inhabited a relatively wide range of habitat types, colonies that have managed to persist in the region have done so equally well in the habitat types represented by the present study. Although our study suggests that the habitat type classifications used in this study were not strong predictors of *A. palmata* colony survival, it is possible that other, more detailed site-level physical habitat characteristics play a role in determining the fate of *A. palmata* colonies.

While it is tempting to surmise that temperature anomalies during the NOAA-recognized periods of El Niño “loading” (summer 2014) and El Niño formation (winter 2014/2015) likely facilitated a cascade of stressors (bleaching, disease) that ultimately resulted in extreme mortality, we were unable to explicitly include bleaching and disease occurrence in the present study. Many colonies that were seemingly healthy with no observed stress responses in one survey event were nevertheless dead by the next survey event. Dynamic stressors such as bleaching and disease can quickly decimate colonies, but unless surveyors observed the actual stressor implicated in a colony’s death, one can only speculate as to

the direct cause of mortality for lost colonies. Colonies in our study were visited, on average, every four months over the 56-month study period. Hence, surveyors had limited opportunities to observe periodic bleaching and disease outbreaks, resulting in uncertainty regarding whether or not dead colonies were exposed to one or both of these stressors (i.e., dead colonies generally do not show evidence of either bleaching or disease). We are currently expanding our modeling approach to incorporate these potentially important stressors, which we hope will help to improve our understanding of their influence on colony survival.

Our findings have potentially important management implications, particularly with respect to propagation and outplanting of *A. palmata* colonies. The important ecosystem functions of *A. palmata*, coupled with its extreme decline, has led to an increase in the use of propagation and outplanting approaches to enhance and restore wild coral populations (Epstein et al. 2003; Miller et al. 2014). While substantial regional efforts to outplant large numbers of *A. palmata*'s faster-growing sister species, *A. cervicornis*, have been met with varying degrees of success (Garrison and Ward 2012; Bruckner 2009; Rinkevich 2000; Shafir et al. 2006; Schopmeyer et al. 2011; Amar and Rinkevich 2007; Johnson et al. 2011; Herlan and Lirman 2008; Miller et al. 2014; Rinkevich 2014; Young et al. 2012; Nedimyer et al. 2011), outplanting attempts for *A. palmata* are in their infancy. Over 10,000 *A. palmata* colonies are currently permitted by the Florida Keys National Marine Sanctuary and Florida Fish and Wildlife Conservation Commission to be relocated to sites in the Florida Keys over the next five years. Where these efforts are concerned, managers and biologists clearly have no control over seasonal or annual climatic conditions, both of which presumably influence the survival of outplanted coral colonies. Managers do, however, have control over when outplanting activities are initiated. Similarly, our study indicates that regional differences in colony survival exist, which may be relevant when managers are deciding where to implement outplanting activities. Additionally, the positive relationship between skeletal area and colony survival suggests that the larger the skeletal area of outplanted colonies, the more likely they are to survive. While it is difficult to identify an optimal colony size that would be most suitable for outplanting, our results strongly suggest that larger colonies are most likely to survive over the long term. We suspect that the optimal choice of outplant size will depend upon where the outplanting activities will occur, the anticipated climatic conditions, and perhaps most importantly, practical limitations associated with the capability and capacity of *A. palmata* rearing facilities. Lastly, although the influence of percent live tissue on colony survival was not explicitly addressed by this

study, maximizing the percent live tissue associated with outplanted colonies would benefit their long term survival.

Acknowledgements

We wish to acknowledge funding for this research received from NOAA/NMFS Species Conservation Grants to States (NA10NMF4720029) and the Office of Protected Resources (NA15NMF4720280). This research was conducted under permits from the Florida Keys National Marine Sanctuary (FKNMS-2010-126 and FKNMS-2013-104), Biscayne National Park (BISC-2010-SCI-0044, BISC-2011-SCI-0026, BISC-2012-SCI-0026, BISC-2014-SCI-0032, and BISC-2015-SCI-0019), Dry Tortugas National Park (DRTO-2010-SCI-0025, DRTO-2011-SCI-0016, DRTO-2012-SCI-0018, DRTO-2013-SCI-0016, DRTO-2014-SCI-0010, and DRTO-2015-SCI-0018). The statements, conclusions, and recommendations expressed herein are those of the authors and do not necessarily reflect the views of the State of Florida, the National Oceanographic Atmospheric Agency, the National Park Service, or the Florida Keys National Marine Sanctuary.

References

- Amar KO, Rinkevich B (2007) A floating mid-water coral nursery as larval dispersion hub: Testing an idea. *Mar Biol* 151:713-18
- Andrews K, Nall L, Jeffrey C, Pittman S, Banks K, Dodge RE, Beaver C, Bohnsack J, Jaap W, Gilliam D, Keller B, Leeworthy VR, Matthews T, Ruiz-Carus R, Santavy D, Spieler R (2005) The state of coral reef ecosystems of Florida. NOAA Technical Memorandum NOS NCCOS 11:150-200
- Aronson RB, Bruckner AW, Moore J, Precht WF, Weil E (2008a) IUCN Red List of Threatened Species: *Acropora cervicornis*. Version 2012.2, Cambridge, United Kingdom: International Union for Conservation of Nature and Natural Resources
- Aronson RB, Bruckner AW, Moore J, Precht WF, Weil E (2008b) IUCN Red List of Threatened Species: *Acropora palmata*. Version 2012.2, Cambridge, United Kingdom: International Union for Conservation of Nature and Natural Resources
- Bak RPM, Meesters EH (1998) Coral population structure: the hidden information of colony size-frequency distributions. *Mar Ecol Prog Ser* 162:301-306
- Barnes BB, Hu C, Schaeffer BA, Lee Z, Palandro DA, Lehrter JC (2013) MODIS-derived spatiotemporal water clarity patterns in optically shallow Florida Keys waters: A new approach to remove bottom contamination. *Remote Sens Environ* 134:377-391

- Baumstark, R.D (2013) Coordinated coral and hardbottom ecosystem mapping, monitoring and management. Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL
- Blanchon P (2010) Reef demise and back-stepping during the last interglacial, northeast Yucatan. *Coral Reefs* 29:481-498
- Blanchon P, Shaw J (1995) Reef drowning during the last deglaciation - evidence for catastrophic sea-level rise and ice-sheet collapse. *Geology* 23:4-8
- Blanchon P, Eisenhauer A (2001) Multi-stage reef development on Barbados during the Last Interglaciation. *Quat Sci Rev* 20:1093-1112
- Brock JC, Palaseanu-Lovejoy M, Wright CW, Nayegandhi A (2008) Patch-reef morphology as a proxy for Holocene sea-level variability, Northern Florida Keys, USA. *Coral Reefs* 27:555-568
- Bruckner AW (2002) Proceedings of the Caribbean Acropora Workshop: Potential application of the U.S. Endangered Species Act as a conservation strategy. NOAA Technical Memorandum NMFS-OPR-24, Silver Spring, MD
- Bythell J, Sheppard C (1993) Mass mortality of Caribbean shallow corals. *Marine Pollution Bulletin* 26:296-297
- Done TJ (1983) Coral zonation: Its nature and significance. In: Barnes DJ (ed) *Perspectives on Coral Reefs*. Australian Institute of Marine Science, Townsville, pp107-147
- Dullo WC (2005) Coral growth and reef growth: a brief review. *Facies* 51:37-52
- Dustan P (1985) Community structure of reef-building corals in the Florida Keys USA Carysfort Reef Key Largo and Long Key Reef Dry Tortugas. *Atoll Research Bulletin* 288:1-29
- Epstein N, Bak RPM, Rinkevich B (2003) Applying forest restoration principles to coral reef rehabilitation. *Aquat Conserv-Mar Freshw Ecosyst* 13:387-395
- Fenner DP (1988) Some leeward reefs and corals of Cozumel, Mexico. *Bull Mar Sci* 42:133-144
- Fitt WK, McFarland FK, Warner ME, Chilcoat GC (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnol. Ocean.* 45: 677-685
- Florida Fish and Wildlife Conservation Commission (2016) Coral Reef Evaluation and Monitoring Project Executive Summary 2016. <http://myfwc.com/research/habitat/coral/cremp/>
- Florida Reef Resilience Program (2016) Disturbance Monitoring Response Monitoring Quick Look Report: Summer 2014. <http://frrp.org/wp-content/uploads/2016/07/2014-Summer-DRM-Quick-Look-Report.pdf>
- Gabriel JJ, Reinhardt EG, Peros MC, Davidson DE, van Hengstum PJ, Beddows PA (2009) Palaeoenvironmental evolution of Cenote Aktun Ha (Carwash) on the Yucatan Peninsula, Mexico and its response to Holocene sea-level rise. *J Paleolimn* 42:199-213
- Gelman, A. J., H. S. Carlin, D. B. Stern, and D. B. Rubin. 2004. *Bayesian Data Analysis*. Chapman and Hall/CRC, New York
- Gladfelter EH, Monahan RK, Gladfelter WB (1978) Growth-rates of 5 reef-building corals in the northeastern Caribbean. *Bull Mar Sci* 28:728-734

- Herlan J, Lirman D (2008) Development of a coral nursery program for the threatened coral *Acropora cervicornis* in Florida. Proc 11th Int Coral Reef Symp Ft Lauderdale: 1244-1247
- Hubbard DK (1989) Terrestrial and Marine Geology of St. Croix Special Publication No 9. West Indies Laboratory, Fairleigh Dickinson Univ, St. Croix, USVI 213
- Hubbard DK (1997) Reefs as dynamic systems. Chapman and Hall, Inc.; Chapman and Hall Ltd.
- Hughes TP (1984) Population dynamics based on individual size rather than age: a general model with a reef coral example. Am. Nat 123:778-795
- Hughes TP, Connel JH (1987) Population dynamics based on size or age? A reef-coral analysis. Am. Nat. 129:8189-829
- Hughes TP, Connel JH (1987) Multiple stressors on coral reefs: A long-term perspective. Limnol Ocean 44:932-940
- Jaap WC, Halas JC, Muller RG (1988) Community dynamics of stony corals (Milleporina and Scleractinia) at Key Largo National Marine Sanctuary, Florida, during 1981-1986. Proc 6th Int Coral Reef Symp Townsville
- Johnson ME, Lusic C, Bartels E, Baums IB, Gilliam GS, Larson L, Lirman D, Miller MW, Nedimyer K, Schopmeyer S (2011) Caribbean *Acropora* restoration guide: best practices for propagation and population enhancement. The Nature Conservancy, Arlington VA
- King, AJ, DC Gwinn, Z Tonkin, J Mahoney, S Raymon, L Beesley (2016) Using abiotic drivers of fish spawning to inform environmental flow management. Journal of Applied Ecology 53:34-43
- Lesser MP (2011) Coral bleaching: causes and mechanisms. In: Dubinsky Z, Stambler N (eds) Coral reefs: an ecosystem in transition. Springer, Dordrecht, pp 405–419
- Lirman D (1999) Reef fish communities associated with *Acropora palmata*: Relationships to benthic attributes. Bull Mar Sci 65:235-252
- Lirman D, Fong P (2007) Is proximity to land-based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract. Marine Pollution Bulletin 54:779-791
- Lunn, D, D Spiegelhalter, A Thomas, N Best (2009) The BUGS project: evolution, critique and future directions. Statistics in Medicine 28:3049-3067
- Manzello DP, Enochs IC, Melo N, Gldhill DK, Johns EM (2012) Ocean acidification refugia of the Florida Reef Tract. PLoS One 7:10
- Manzello DP (2015) Rapid Recent Warming of Coral Reefs in the Florida Keys. Sci. Rep. 5, 16762;doi: 10.1038/srep16762
- Mass T, Kline DI, Roopin M, Veal CJ, Cohen S, Iluz D, Levy O (2010) The spectral quality of light is a key driver of photosynthesis and photoadaptation in Stylophora pistillata colonies from different depths in the Red Sea. J Exp Biol 213:4084-4091
- Miller MW, Bourque AS, Bohnsack JA (2002) An analysis of the loss of acroporid corals at Looe Key, Florida, USA: 1983-2000. Coral Reefs 21:179-182

- Miller MW, Lohr KE, Cameron CM, Williams DE, Peters EC (2014) Disease dynamics and potential mitigation among restored and wild staghorn coral, *Acropora cervicornis*. PeerJ 2:30
- National Marine Fisheries Service (2006) Endangered and threatened species: final listing determinations for elkhorn coral and staghorn coral. Federal Register 71:26852-26872
- Nedimyer K, Gaines K, Roach S (2011) Coral Tree Nursery: An innovative approach to growing corals in an ocean-based field nursery. Int J of the Bioflux Soc 4:442-446
- Porter JW, Meier OW (1992) Quantification of loss and change in Floridian reef coral populations. Am Zool 32:625-640
- Raymundo LJ, Maypa AP (2004) Getting bigger faster: mediation of size-specific mortality via fusion in juvenile coral transplants. Ecol Appl 14:281-295
- Rinkevich B (2000) Steps towards the evaluation of coral reef restoration using small branch fragments. Mar Biol 136:807-12
- Rinkevich B (2014) Rebuilding coral reefs: does active restoration lead to sustainable reefs? Curr. Opin. Env. Sust. 7:28-36
- Royle JA, Dorazio RM (2008) Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations, and Communities. Academic Press, New York p 356.
- Ruzicka RR, Colella MA, Porter JW, Morrison JM, Kidney JA, Brinkhuis V, Lunz KS, Macaulay KA, Bartlett LA, Meyers MK, Colee J. (2013) Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. Mar Ecol Prog Ser 489:124-141
- Schmidt JH, Walker JA, Lindberg MS, Johnson DS, Stephens SE (2010) A general Bayesian hierarchical model for estimating survival of nests and young. The Auk 127:379-386
- Schopmeyer SA, Lirman D, Bartels E, Byrne J, Gilliam DS, Hunt J, Johnson ME, Larson, EA, Maxwell K, Nedimyer K, Walter C (2012) In Situ Coral Nurseries Serve as Genetic Repositories for Coral Reef Restoration after an Extreme Cold-Water Event. Restor Ecol 20:696-703
- Shafir S, Rijn JV, Rinkevich B (2006) Steps in the construction of underwater coral nursery: An essential component in reef restoration acts. Mar Biol 149:670-87
- Shinn EA (2004) The mixed value of environmental regulations: do acroporid corals deserve endangered species status? Mar Pollut Bull 49:531-533
- Shinn EA, Lidz BH, Halley RB, Hudson JH, Kindinger JL (1989) Reefs of Florida and the Dry Tortugas field trip guidebook T176. AGU, Washington D.C. 57
- Smith LD, Hughes TP (1999) An experimental assessment of survival, re-attachment and fecundity of coral fragments. J Exp Mar Biol Ecol 235:147-164.
- Toscano MA, Lundberg J (1998) Early Holocene sea-level record from submerged fossil reefs on the southeast Florida margin. Geology 26:255-258
- Toscano MA, Macintyre IG (2003) Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated C-14 dates from *Acropora palmata* framework and intertidal mangrove peat. Coral Reefs 22:257-270
- Veron JEN (2000) Corals of the World. Australian Institute of Marine Science, Townsville MC, Qld, Australia

- Walker BK (2012) Spatial analyses of benthic habitats to define coral reef ecosystem regions and potential biogeographical boundaries along a latitudinal gradient. *PloS One* 7:e30466
- Wells J (1957) Coral Reefs Geological Society of America Memoirs 67. Geological Society of America, U.S.A., pp609-631
- Williams DE, Miller MW, Kramer KL (2006) Demographic monitoring protocols for threatened Caribbean *Acropora* spp. corals. NOAA Technical Memorandum NMMFS-SEFSC-543, Miami, FL, p 112
- Williams DE, Miller MW (2012) Attributing mortality among drivers of population decline in *Acropora palmata* in the Florida Keys. *Coral Reefs* 31: 369-382
- Wirt K, Hallock P, Palandro D, Lunz K (2015) Potential habitat of *Acropora* spp. on reefs of Florida, Puerto Rico, and the U.S. Virgin Islands. *Global Ecology and Conservation* 3:242-255
- Wirt Ames K (2016) *Acropora* habitat evaluation and restoration site selection using a species distribution modeling approach. Ph.D. thesis, University of South Florida, College of Marine Science
- Yentsch CS, Yentsch CM, Cullen JJ, Lapointe B, Phinney DA, Yentsch SW (2002) Sunlight and water transparency: cornerstones in coral research. *J Exp Mar Biol Ecol* 268:171-183
- Young CN, Schopmeyer SA, Lirman D (2012) A review of reef restoration and coral propagation using the threatened genus *Acropora* in the Caribbean and western Atlantic. *Bull Mar Sci* 88: 1075-1098