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RESEARCH ARTICLE

Differential survival of nursery-reared *Acropora cervicornis* outplants along the Florida reef tract

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In recent decades, the Florida reef tract has lost over 95% of its coral cover. Although isolated coral assemblages persist, coral restoration programs are attempting to recover local coral populations. Listed as threatened under the Endangered Species Act, *Acropora cervicornis* is the most widely targeted coral species for restoration in Florida. Yet strategies are still maturing to enhance the survival of nursery-reared outplants of *A. cervicornis* colonies on natural reefs. This study examined the survival of 22,634 *A. cervicornis* colonies raised in nurseries along the Florida reef tract and outplanted to six reef habitats in seven geographical subregions between 2012 and 2018. A Cox proportional hazards regression was used within a Bayesian framework to examine the effects of seven variables: (1) coral-colony size at outplanting, (2) coral-colony attachment method, (3) genotypic diversity of outplanted *A. cervicornis* clusters, (4) reef habitat, (5) geographical subregion, (6) latitude, and (7) the year of monitoring. The best models included coral-colony size at outplanting, reef habitat, geographical subregion, and the year of monitoring. Survival was highest when colonies were larger than 15 cm (total linear extension), when outplanted to back-reef and fore-reef habitats, and when outplanted in Biscayne Bay and Broward–Miami subregions, in the higher latitudes of the Florida reef tract. This study points to several variables that influence the survival of outplanted *A. cervicornis* colonies and highlights a need to refine restoration strategies to help restore their population along the Florida reef tract.

Key words: *Acropora cervicornis*, coral reef, coral restoration, coral-colony size, corals, Florida, habitat, nursery-reared outplants, survival, threatened species

Implications for Practice

- Historically common along the Florida reef tract, populations of *Acropora cervicornis* are now relatively sparse and therefore coral restoration programs are attempting to promote population recovery.
- Data from six coral restoration programs along the Florida reef tract showed that *A. cervicornis* colonies >15 cm outplanted in moderate-flow habitats had the highest likelihood of survival.
- It is recommended to outplant *A. cervicornis* colonies into nearshore habitats of Broward–Miami and Biscayne Bay where they may glean some added protection from coral bleaching as ocean temperatures continue to increase.
- Coral restoration programs should plan to factor long-range forecasts of thermal-stress events and hurricanes into their structure.

Introduction

Over the last four decades, thermal-stress events and disease have caused rapid declines in coral populations worldwide (Edwards & Gomez 2007; Hoegh-Guldberg et al. 2007; Hughes et al. 2018). Some of the most heavily impacted regions have been the Caribbean (Aronson & Precht 2001) and Florida (Porter & Meier 1992; Toth et al. 2014; Precht et al. 2016; Walton

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et al. 2018). This decline included unprecedented mortality of *Acropora cervicornis* and *Acropora palmata*, two historically important reef-building coral species in the Caribbean. Historically, in Florida, *A. palmata* was dominant on reef crests on fore reefs, and *A. cervicornis* was dominant between 5 and 25 m on fore reefs and in shallower habitats on sheltered patch and back reefs (Agassiz 1885; Vaughan 1919; Goldberg 1973; Marszalek et al. 1977; Precht & Miller 2007). However, both acroporids suffered major declines because of white-band disease in the late 1970s and early 1980s (Aronson & Precht 2001; Gardner et al. 2003). More recently the coral assemblages along the Florida reef tract have become homogeneous (Burman et al. 2012) with the loss of reef-building species such as acroporids (Precht & Miller 2007). In 2006, their population declines prompted the listing of both acroporid species as threatened under the U.S. Endangered Species Act (NMFS 2006), and in 2008 as critically endangered and placed on the International Union for Conservation of Nature red list (IUCN 2020). Four decades after the initial mortality events, acroporid populations along the Florida reef tract continue to decline (Ruzicka et al. 2013; Toth et al. 2014).

To facilitate the recovery of acroporid populations, coral restoration programs have expanded along the Florida reef tract over the last 15 years (Johnson et al. 2011; Schopmeyer et al. 2012; Young et al. 2012). These restoration programs have focused particularly on restoring populations of *A. cervicornis* (Goergen et al. 2019; Ware et al. 2020). Although coral restoration may be a useful option to increase coral populations, strategies to optimize survival of nursery-reared outplants are still in their infancy. Previous studies have shown a positive relationship between colony size and survival of natural coral populations (Hughes et al. 1992), and several restoration studies have also shown that colonies with greater than 15 cm total linear extension (TLE) survive better than smaller colonies (Bowden-Kerby 2001; Herlan & Lirman 2008; Lirman et al. 2014; Goergen & Gilliam 2018). Yet, large colonies take longer to grow in nurseries than small colonies, and outplanting small colonies is often most practical. Attachment method could also play a role in survival. Some studies suggest that the "nail" method is the most efficient (Bruckner & Hourigan 2000; Young et al. 2012; Goergen & Gilliam 2018), the most inexpensive (Goergen & Gilliam 2018), and the most stable method for coral restoration in high-energy environments (Bruckner & Hourigan 2000; Young et al. 2012). Still, the epoxy method is convenient in moderate- to low-energy environments especially when coral colonies are large.

Coral survival is also a consequence of genotypic tolerance (Drury et al. 2017), and bet-hedging theory suggests that diverse clusters of *A. cervicornis* outplants should have the highest likelihood of survival (Hughes et al. 2008). Environmental differences across habitats and regions, such as differences in flow regimes and irradiance, are also likely to influence survival of coral outplants, especially since spatial differences in environmental conditions influence natural distributions of *A. cervicornis* (Marszalek et al. 1977; Ginsburg & Shinn 1995; Toth et al. 2018; van Woesik et al. 2020). Historically, *A. cervicornis* was ubiquitous in clear oligotrophic waters (Precht & Miller 2007), although recent studies suggest that turbid conditions are favorable during high-heat stress events (van Woesik & McCaffrey 2017). Therefore, nearshore reefs may become important habitats for the restoration of *A. cervicornis* along the Florida reef tract as the ocean temperatures continue to increase.

In order to facilitate the recovery of coral populations, restoration programs need answers to a suite of questions, which include: (1) What is the optimal size of an outplanted coral colony? (2) Which attachment method is best for outplanting nursery-reared colonies to natural reefs? and (3) Which habitats and geographical locations will show the highest survival? Here, we compile data from six different coral restoration programs throughout Florida to determine the conditions that may influence the survival of 22,634 nursery-reared outplanted *A. cervicornis* colonies. The colonies were outplanted to six natural reef habitats in seven geographical subregions along the Florida reef tract between 2012 and 2018. The objectives of the study were to examine the influence of seven variables on survival, which included: (1) coral-colony size at outplanting, (2) coral-colony attachment method, (3) genetic diversity of outplanted *A. cervicornis* clusters, (4) reef habitat, (5) geographical subregion, (6) latitude, and (7) the year of monitoring.

Methods

We collated data on the survival of 22,634 *Acropora cervicornis* colonies raised in nurseries along the Florida reef tract and outplanted to six natural reef habitats in seven geographical subregions between 2012 and 2018 from the following six coral restoration programs (i.e. organizations, agencies, or universities): (1) The Nature Conservancy, (2) the Mote Marine Laboratory, (3) the Florida Fish and Wildlife Conservation Commission, (4) the Coral Restoration Foundation, (5) the University of Miami, and (6) Nova Southeastern University (Fig. 1; Table 1; extended details of methods are provided in Supplement S1). This current study examined the relationships between the survival of the *A. cervicornis* colony outplants and the effects of seven variables: (1) coral-colony size at outplanting, (2) coral-colony attachment method, (3) genetic diversity of outplanted *A. cervicornis* clusters, (4) reef habitat, (5) geographical subregion, (6) latitude, and (7) the year of monitoring.

The six different coral restoration programs identified in this study used either one of two methods for documenting the size of *A. cervicornis* colonies. While most of the groups reported the size of *A. cervicornis* colonies in terms of TLE (Johnson et al. 2011), which is the sum of the lengths of all the branches, the Coral Restoration Foundation reported maximum colony diameter. Therefore, the Coral Restoration Foundation maximum diameter measurements were aligned (using $TLE = 2.95*diameter - 9.17$) to the TLE size-class categories used in this study: (1) 1–15 cm TLE were classified as small colonies, (2) 16–50 cm TLE were classified as medium colonies, and (3) 51–160 cm TLE were classified as large colonies (Table 1).

All six coral restoration programs prepared the point of coral attachment by clearing the algae and sediment-bound turf with scrubbers from the specific area where corals were to be outplanted, then used either one, or both, of two attachment

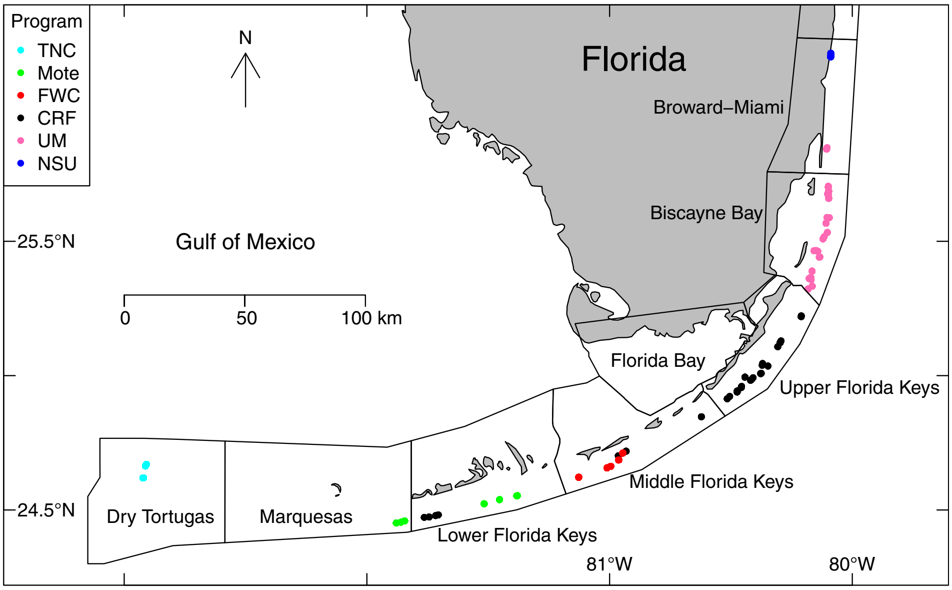

Figure 1. Locations of *Acropora cervicornis* colony outplant sites (<8 m) along the Florida reef tract from 2012 to 2018 color-coded by coral restoration program abbreviated as The Nature Conservancy (TNC), Mote Marine Laboratory (Mote), Florida Fish and Wildlife Conservation Commission (FWC), Coral Restoration Foundation (CRF), University of Miami (UM), and Nova Southeastern University (NSU).

Table 1. Size classes of the 22,634 *Acropora cervicornis* colony outplants used in this study from each of six coral restoration programs along the Florida reef tract from 2012–2018. For comparative purposes, this study converted the coral restoration foundation maximum diameter measurements to three standard size-class categories calculated according to total linear extension (TLE): (i) small colonies 1–15 cm TLE, (ii) medium colonies 16–50 cm TLE, and (iii) large colonies 51–160 cm TLE.

	Number of Outplants	*Small (1–15 cm)*	*Medium (16–50 cm)*	*Large (51–160 cm)*	*Years of Outplanting and Monitoring*
The Nature Conservancy	2,380	10 cm	15–25 cm	-	4/2012–8/2017
Mote Marine Laboratory	15,917	-	15–20 cm 16–30 cm 31–50 cm	51–100 cm	7/2014–9/2018
Florida Fish and Wildlife	972	0–5 cm 5–10 cm	20–50 cm	51–100 cm	4/2012–4/2017
Coral Restoration Foundation	1,220	Maximum diameter	Maximum diameter	Maximum diameter	1/2016–5/2018
University of Miami	1,740	Exact length (cm)	Exact length (cm)	Exact length (cm)	5/2012–10/2017
Nova Southeastern University	405	5–15 cm	16–35 cm 36–60 cm	61–160 cm	3/2015–4/2016

methods: (1) nail and cable tie and (2) epoxy. The nail and cable-tie method involved hammering a masonry nail vertically into the reef substrate and securing a fragment of *A. cervicornis* to the nail with cable ties (Fig. 2). The epoxy method involved adhering a colony directly to the reef substrate with a small amount of epoxy. The Nature Conservancy, the Mote Marine Laboratory, the University of Miami, and Florida Fish and Wildlife used nail and cable ties. The Coral Restoration Foundation used epoxy, and Nova Southeastern University included data on both methods (Table 1).

Coral host genotypes were characterized using four host (diploid) microsatellite markers following Baums et al. (2005). The current study tested whether the aggregation of genotypic diversity in clusters of *A. cervicornis* outplants influenced their survival (Drury et al. 2019; see Supplement S1 for details of clustering). The number of *A. cervicornis* genotypes in each cluster of outplanted coral colonies at each reef habitat were examined using three classes of genotypic diversity: (1) high (≥21 genotypes), (2) moderate (7–20 genotypes), and (3) low (<7 genotypes).

A. cervicornis colonies were outplanted by the six different coral restoration programs at six standardized reef habitats along the Florida reef tract between 2012 and 2018 (Florida Fish and Wildlife habitat shapefiles, https://myfwc.com/research/gis/regional-projects/unified-reef-map) in <8 m water: (1) back reefs, (2) bank/shelf, (3) fore reefs, (4) lagoons (i.e. patch reefs), (5) reef crest, and (6) unknown or unidentified habitats.

Figure 2. Outplanting techniques of *Acropora cervicornis* colonies involved two different attachment methods: (1) the nail and cable-tie method and (2) the epoxy method. The top two images show the nail and cable-tie method, the bottom left image shows the epoxy method, and the bottom right panel shows a combination of both methods. All photos by Dalton Helsey, University of Miami, except for the bottom left photo, which was taken by Liz Goergen.

In addition to being outplanted at six different reef habitats, *A. cervicornis* colonies were distributed across seven different geographical locations of the Florida reef tract, herein called subregions: (1) Dry Tortugas, (2) Marquesas, (3) lower Florida Keys, (4) middle Florida Keys, (5) upper Florida Keys, (6) Biscayne Bay, and (7) Broward–Miami (Fig. 1). All outplanted *A. cervicornis* colonies analyzed in this study were considered shallow (<8 m) outplants. To examine a potential trend with latitude, the outplant sites were designated a latitude and longitude coordinate, and each outplant site was categorized into one of five latitudinal ranges: 24°–24.5°N, >24.5°–25°N, >25°–25.5°N, >25.5°–26°N, >26°–26.5°N.

All six coral restoration programs monitored the survival of *A. cervicornis* outplants along the Florida reef tract between 2012 and 2018. All programs monitored outplants after 1 month and 1 year, whereas only some programs monitored annually for 4 years. At every monitoring interval, each outplanted colony was visually assessed to determine if it was alive or dead. An *A. cervicornis* colony was considered censored, which is the terminology used in the medical literature, if the colony was still alive at the last monitoring interval.

Data Analysis

A semi-parametric Cox proportional hazards regression was used within a Bayesian framework to examine the survival of *A. cervicornis* outplants. The technique is a rigorous model that determines the effects of different covariates on the outcome of survival; it is semi-parametric because it has the advantage of the baseline hazard taking any form whereas the covariates are linear. We were interested in determining the relative risk of mortality that may have been attributed to the following seven covariates: (1) coral-colony size at outplanting (three levels), (2) coral-colony attachment method (two levels), (3) genotypic diversity of outplanted *A. cervicornis* clusters (three levels), (4) reef habitat (six levels), (5) geographical subregion (seven levels), (6) latitude (five levels), and (7) the year of outplanting (six levels). The Cox proportional hazards model is represented as:

$$h_i(t) = h_0(t)\exp^{(B_1 x_{i1} + B_2 x_{i2} \ldots + B_k x_{ik})} \tag{1}$$

where h_i is the hazard at observation i at time t, h_0 is the baseline hazard (when all covariates are equal to zero), B_i are the intercepts, and x_i are the environmental covariates of interest. The model was used to quantify the relative risk attributed to each covariate on the likelihood of *A. cervicornis* survival. The analyses were run in "spBayesSurv" (Zhou et al. 2018) in R (R Core Team 2019) using noninformative priors. Multiple models were run to find the most informative model, with the highest log-pseudo marginal likelihood. Latitude was examined using a Cox proportional hazards model that was independent of subregional effects (but included colony size, habitat, and year), because of the confounding effects between latitude and subregions.

The models captured the effects of multiple covariates on coral survival; however, when a covariate showed an effect we did not pool that data with other covariates. Therefore, we graphically display the response of *A. cervicornis* outplant survival for similar habitats and subregions for the year 2016. Although the year 2016 was one of the best years for survival, it was also the year when all six agencies were simultaneously monitoring survival. The results for other habitats, subregions, and years are presented in supplementary document. The R script files and data files can be located at https://github.com/rvanwoesik/Acropora_survival.

Results

The most optimal Cox proportional hazards model that assessed the survival of *Acropora cervicornis* outplants along the Florida reef tract between 2012 and 2018, with the highest log-pseudo-marginal likelihood, included the variables coral-colony size at outplanting, reef habitat, geographical subregion, and the year of monitoring. The highest survival of *A. cervicornis* outplants was apparent for medium-sized colonies, 16–50 cm TLE, and large-sized colonies, 51–160 cm TLE (Fig. 3; Table 2, Supplement S1, Figs. S6–S11). Small-sized colonies, between 1 and 15 cm TLE, showed lower survival than medium- and large-sized colonies (Fig. 3; Table 2). Although survival was not vastly different across habitats, the Cox proportional hazards model did indicate that back-reef and fore-reef habitats showed the highest level of survival of *A. cervicornis* outplants (Fig. 4), with lowest survival on the reef crest (Table 2, Supplement S1).

The results of the Cox proportional hazards model also considered survival of *A. cervicornis* outplants in geographical subregions independently of coral colony size, reef habitat, and year of monitoring (Table 2). These results indicated that the overall survival of *A. cervicornis* outplants in the different subregions (listed from the highest to the lowest likelihood of survival) occurred in the Biscayne Bay and Broward–Miami subregions; followed by the Dry Tortugas, the lower Florida Keys, and the Marquesas subregions; and then the middle and upper Florida Keys. Even when considering the variables coral-colony size, reef habitat, and year of monitoring, together with geographical subregions, Biscayne Bay, Broward–Miami, and the Dry Tortugas subregions still consistently exhibited the highest survival of *A.cervicornis* outplants (Fig. 5, Supplement S1, Figs. S6–S17).

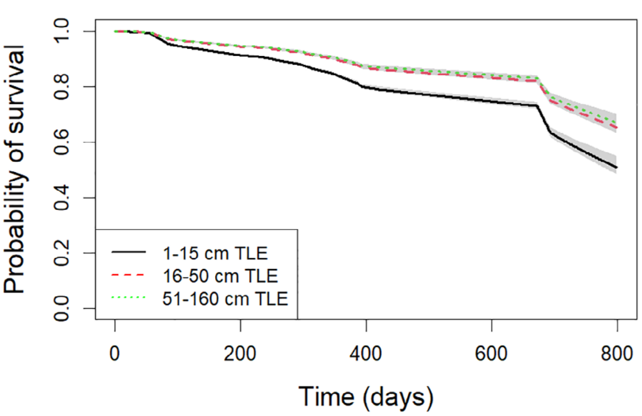

Figure 3. Survival by size class of *Acropora cervicornis* colonies outplanted to fore-reef habitats (<8 m) in the lower Florida Keys, in 2016. The three standard size-class categories were calculated according to total linear extension (TLE). Shadings are the 95% credible intervals.

The years with the highest survival for *A. cervicornis* outplant survival were 2012 and 2016, and the years with the lowest survival were 2018, 2017, and 2014 (Table 2). Examining survival across latitudes using a pooled Cox proportional hazards model (without including the covariate subregions, but including colony size, reef habitat, and year of monitoring) suggested that although there was considerable overlap in credible intervals, survival of *A. cervicornis* outplants increased with increasing latitude along the Florida reef tract (Fig. 6).

Including coral-colony attachment method and genotypic diversity of outplanted *A. cervicornis* clusters within the model decreased the log-pseudo marginal likelihood value, suggesting that these two predictive variables did not have a major measured effect on *A. cervicornis* outplant survival along the Florida reef tract between 2012 and 2018.

Discussion

This study found that five variables—namely, coral-colony size at outplanting, reef habitat, geographical subregion, latitude, and the year of monitoring—influenced the survival of nursery-reared *Acropora cervicornis* colonies that were outplanted to reefs along the Florida reef tract between 2012 and 2018. By contrast, coral-colony attachment method and genotypic diversity of outplanted *A. cervicornis* clusters did not have significant effects on outplant survival. Therefore, when identifying outplanting sites, coral restoration programs should not rely solely upon historical distributions of *A. cervicornis* but rather take into consideration contemporary niche space (van Woesik et al. 2020) and the suite of variables identified by this study.

Considering coral-colony size at outplanting, medium- (16–50 cm TLE) and large-sized (51–160 cm TLE) *A. cervicornis* outplants had higher survival rates than small-sized (<15 cm TLE) outplants. It is uncertain whether clipping the small colonies from large nursery-reared colonies created any further disadvantage to the outplanted fragments by limiting resources. Small *Acropora* colonies, however, are known to have generally lower survival than large coral colonies of the same species (Hughes et al. 1992), in part because they are more vulnerable than larger colonies to disturbances, such as predation by fireworms (*Hermodice carunculata*; Goergen et al. 2019) or by gastropods (*Coralliophila abbreviata*; Goergen & Gilliam 2018), abrasion by gorgonians (Sebens & Miles 1988), the presence of macroalgae (van Woesik et al. 2017), and by sedimentation (De Marchis 2017). These disturbances can cause partial coral colony mortality, which have disproportionate consequences on small colonies, that can lead to total colony mortality (van Woesik & Jordán-Garza 2011). Indeed, small colonies are generally disadvantaged on coral reefs (Hughes et al. 1992) except during thermal-stress events when small colonies have an advantage because of comparatively high rates of mass transfer (Patterson 1992; Loya et al. 2001; Nakamura & van Woesik 2001).

Table 2. Posterior inference of regression coefficients of the Cox proportional hazards model, using large-sized *Acropora cervicornis* colony outplants (51–160 cm TLE) inputting the data from six coral restoration programs from 2012–2018 along the Florida reef tract. TLE refers to total linear extension (Johnson et al. 2011), which is the sum of the lengths (cm) of all the branches. The six coral restoration programs included: (1) The Nature Conservancy, (2) the Mote Marine Laboratory, (3) the Florida Fish and Wildlife Conservation Commission, (4) the Coral Restoration Foundation, (5) the University of Miami, and (6) Nova Southeastern University. The 23 records from 2013 were removed for this analysis. The bases for the models were: large colonies, back reef, Biscayne Bay, and the year 2012.

		Mean	*Median*	*SD*	*95% CI-Low*	*95% CI-Upper*
Outplant size	Medium	0.1106	0.1103	0.0033	0.1052	0.1182
	Small	0.5058	0.5052	0.0151	0.4815	0.5408
Reef habitat	Bank/shelf	0.3112	0.3105	0.0093	0.2960	0.3324
	Fore reef	0.0190	0.0189	0.0006	0.0180	0.0203
	Lagoon	0.1971	0.1971	0.0058	0.1880	0.2115
	Reef crest	0.3759	0.3759	0.0111	0.3581	0.4023
	Unknown	0.2763	0.2765	0.0080	0.2644	0.2964
Geographical subregion	Broward-Miami	−0.1638	−0.1634	0.0067	−0.1754	−0.1532
	Dry Tortugas	1.4690	1.4680	0.0436	1.3989	1.5711
	Lower Keys	1.5276	1.5269	0.0453	1.4549	1.6339
	Marquesas	1.3835	1.3833	0.0410	1.3178	1.4801
	Middle Keys	1.9176	1.9160	0.0572	1.8257	2.0506
	Upper Keys	1.9616	1.9602	0.0583	1.868	2.0976
Year	2014	1.0728	1.0719	0.0318	1.0216	1.1470
	2015	0.6266	0.6267	0.0185	0.5969	0.6706
	2016	0.3293	0.3294	0.0097	0.3139	0.3524
	2017	1.0174	1.0168	0.0302	0.9688	1.0882
	2018	2.5399	2.5421	0.0749	2.4239	2.7195

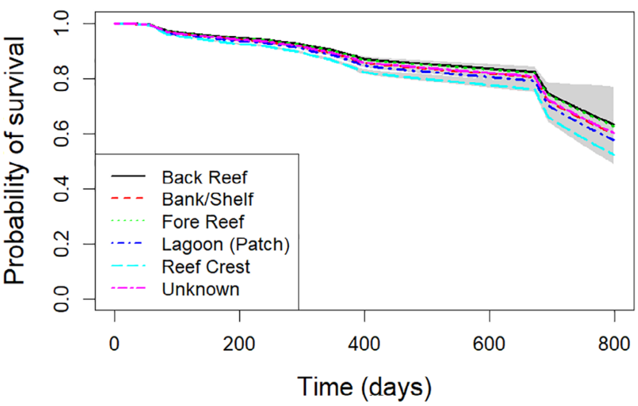

Figure 4. Survival of medium sized (16–50 cm total linear extension) *Acropora cervicornis* colonies outplanted across six different reef habitats (<8 m) in the lower Florida Keys, in 2016. Shadings are the ±95% CI.

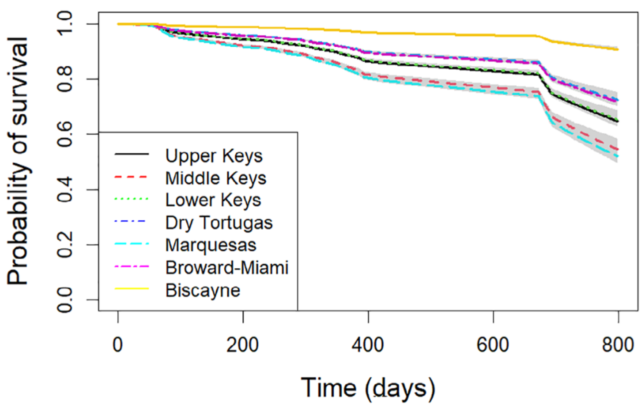

Figure 5. Survival of medium-sized (16–50 cm total linear extension) *Acropora cervicornis* colonies outplanted in fore-reef habitats (<8 m) along seven geographical subregions of the Florida reef tract, in 2016. Shadings are the ±95% CI.

The current study also showed that survival of *A. cervicornis* colonies outplanted to back-reef and fore-reef habitats was higher than survival of colonies outplanted elsewhere. *A. cervicornis* outplants had the lowest survival on highly exposed reef crests, which is not surprising because historically *A. cervicornis* has not been a reef-crest species (Precht & Miller 2007). Coral reef habitats vary in a variety of features, most characteristically differing in flow rates and irradiance (Done 1983). Average flow rates affect rates of mass transfer of metabolites and gases that directly influence coral physiology and survival (Patterson 1992; van Woesik et al. 2012). D'Antonio et al. (2016) showed that contemporary colonies of *A. cervicornis* along the Florida reef tract were most commonly found close to reef edges, where water-flow rates were high. In addition, van Woesik et al. (2020) showed that moderate wave energy, between 0.5 and 1.5 kJ/m^2, and moderate turbidity, between 0.15 and 0.25 kd490 (per m), were the best predictors of site occupancy of *A. cervicornis* along the Florida reef tract. Physiological experiments have also shown that *Acropora* colonies are particularly intolerant to stagnant waters (Nakamura & van Woesik 2001). Therefore, outplanting *A. cervicornis* colonies into low-flow habitats, with low rates of mass transfer, is likely to reduce survival, whereas outplanting them into moderate-flow environments is likely to increase their survival.

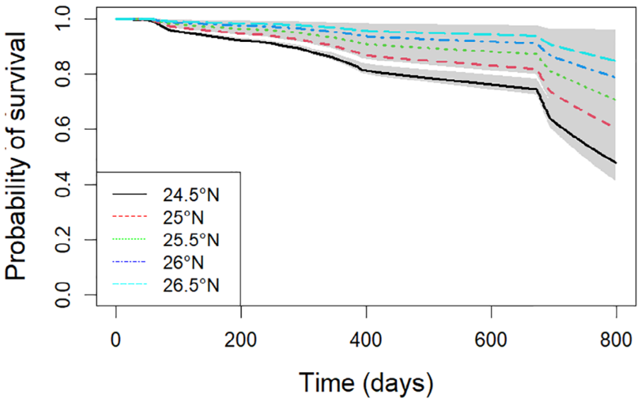

Figure 6. Survival of *Acropora cervicornis* colonies outplanted across five different latitudes, across all three size classes, across all six reef habitats (<8 m) along the Florida reef tract, in 2016. Shadings are the ±95% CI.

The present study identified Biscayne Bay, Broward–Miami, the Dry Tortugas, then the lower Florida Keys subregions as geographical subregions where the likelihood of survival of *A. cervicornis* outplants is highest. These results agree with recent niche models that show the highest probability of occurrence of colonies of *A. cervicornis* are in the Dry Tortugas, the lower Florida Keys, Biscayne Bay, and Broward–Miami, although the niche model also showed a high probability of occurrence in the upper Florida Keys; and that the middle Florida Keys is less likely to support *A. cervicornis* (van Woesik et al. 2020). The present study also found a low likelihood of survival in the middle Florida Keys. Previously, Ginsburg and Shinn (1995) reported on the negative influence of Florida Bay on the middle Florida Keys, and Toth et al. (2018) showed geological evidence that the negative influences of Florida Bay terminated reef accretion in the middle Florida Keys considerably earlier than elsewhere. We suspect, therefore, that Florida Bay may continue to have negative influences on *A. cervicornis* restoration efforts in the middle Florida Keys.

We also found an increase in survival with increasing latitude. The conditions that change with increasing latitude, such as lower maximum sea-surface temperatures or higher nearshore turbidity along the northern Florida reef tract, could moderate the effects of thermal-stress events (van Woesik & McCaffrey 2017). Yet, there are some potentially confounding effects associated with latitude in this study. For example, the six different coral restoration programs work in different subregions, except for the Coral Restoration Foundation, which works in both the upper and lower Florida Keys. Therefore, the latitudinal and subregional effects could be a consequence of some other latent effects that were not quantified here, such as the conditions in the nurseries from which the corals originated, impacts related to the transportation of corals for outplanting, or different suites of genotypes. Indeed, coral physiology may be influenced by nursery conditions, such as water quality, temperature, light, or currents, and survival may be partially dependent on the coupling between the nursery conditions and the reef conditions. Predictions of coral survival therefore may benefit from more information from nursery sites, such as light dynamics, water-flow rates, and diseases.

This study identified the year of outplanting as a significant influence on the survival of *A. cervicornis* colony outplants along the Florida reef tract. It is not necessarily the years themselves that offer any predictive significance, but rather the conditions during each year that influence survival. For example, the worst years for survival of *A. cervicornis* outplants were 2018, 2017, and 2014. In September 2017, Hurricane Irma severely affected the study area (personal observations), particularly the Florida Keys, altering the physical structure of many reefs and increasing sedimentation and turbidity. The survival of *A. cervicornis* coral outplants through Hurricane Irma was higher on patch reefs than on fore reefs (Lohr et al. 2020), which agrees with the impacts of hurricanes to Florida reefs from past studies (Lirman & Fong 1996). In addition, high thermal-stress conditions were associated with the 2014–2017 El-Niño conditions with back-to-back bleaching events occurring in 2014 and 2015 (Manzello 2015; Drury et al. 2017). The summer and winter sea-surface temperatures of 2014 were the highest on record, resulting in a coral-bleaching event throughout the Florida Keys (Manzello 2015). Although Drury et al. (2017) showed high thermal stress and coral bleaching in 2015 in the Florida Keys, our results show higher coral survival in 2015 than in 2014.

The inclusion of the two variables, coral-colony attachment method (either nails and cable-ties or epoxy) and genotypic diversity of outplanted *A. cervicornis* clusters, reduced the model's overall strength. In other words, these two variables did not significantly influence the survivorship of outplanted *A. cervicornis* colonies. However, the effects of genotypic diversity of outplanted *A. cervicornis* clusters on their survival are complex. In theory, and over the long term, genotypically diverse clusters of *A. cervicornis* outplants would be more likely to survive stress events or disease outbreaks than less diverse clusters of outplants (Hughes et al. 2008; Vollmer & Kline 2008). However, survival may be less dependent on the number of genotypes present than on the types of genotypes present and their tolerance to environmental stress (Baums et al. 2010; Drury et al. 2017, 2019). Moreover, our study lacked consistent methodological data on the nature of coral outplant clusters at restoration sites. Ensuring consistency in future studies could contribute toward a better understanding of coral outplant survival. Coral restoration programs therefore need to develop a coordinated effort to record clusters and investigate the role that different genotypes of outplanted *A. cervicornis* colonies have on population restoration efforts along the Florida reef tract (Drury et al. 2017). Key to those studies is a need to relate epigenetic and genetic profiles with phenotypic responses through environmental-stress events (Johnson et al. 2011; van Oppen et al. 2015; Muller et al. 2018).

Although the present study found both significant trends and differences between the survival of nursery-reared *A. cervicornis* colonies outplanted by six coral restoration programs, it also clearly indicated a need for standardized monitoring. This study used data on the survival of individually tagged *A. cervicornis* colony outplants to ensure that each colony was reidentified in the field. This approach, however, may have resulted in an underestimation of outplant survival and overall outplant biomass, either because some outplants may have been dislodged from their holdfasts (Goergen & Gilliam 2018) or because they may have become fragmented over time and survived at some distance from the original outplant locality. Most of the coral restoration programs did not record the dislodged outplants because they were difficult to distinguish from natural fragments. Standardized monitoring that goes beyond tracking individual fragments would greatly benefit coral restoration efforts in the future.

We acknowledge the complexity of understanding coral-outplant survival, especially as the discipline of coral restoration is still in its infancy. Just as importantly, we acknowledge the complexity of choices and decisions taken when analyzing such a complex dataset such as ours through the "garden of forking paths" (Gelman & Loken 2014). For example, a more geographically focused approach may have led to stronger inference, but we would have lost valuable insight on differential survival across the region. In addition, the seven predictive variables examined in the present study are not exhaustive, and future studies may ignore some of the variables, such as attachment method, and target others, such as genotype. We used noninformative priors throughout the analysis because of the sparseness of prior data in this newly emerging field of coral restoration, whereas weakly informative regularizing priors may have provided stronger inference (Banner et al. 2020). Indeed, eliciting informative priors is a highly recommended analytical approach for future coral restoration studies. While our results provide broad insight on the survival of coral outplants (and our analytical approach has been annotated for reproducibility), it is recommended that future studies build on this work by using more extensive and standardized field data and by applying other analytical approaches (Gabry et al. 2019) that may further optimize restoration efforts and enhance populations of endangered coral species.

In conclusion, the present study identified that five variables, namely coral-colony size at outplanting, reef habitat, geographical subregion, latitude, and the year of monitoring, all influenced the survival of nursery-reared *A. cervicornis* outplants. However, coral-colony attachment method and genotypic diversity of outplanted *A. cervicornis* clusters did not significantly influence the survivorship of *A. cervicornis* outplants in natural reef habitats. We recommend continued communication and coordination across all six coral restoration programs to allow for: (1) standardized monitoring, (2) the examination of effects of genotype and phenotypic expression on coral outplant survival, and (3) the determination of optimal macro- and micro-environments for restoring populations of *A. cervicornis* and other corals along the Florida reef tract.

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LITERATURE CITED

Agassiz A (1885) Explorations of the surface fauna of the Gulf Stream, under the auspices of the United States Coast Survey II. Memoirs of the American Academy of Arts and Sciences 11:106–133

Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460:25–38

Banner K, Irvine K, Rodhouse T (2020) The use of Bayesian priors in ecology: the good, the bad and the not great. Methods in Ecology and Evolution 11:882–889

Baums IB, Miller MW, Hellberg ME (2005) Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. Molecular Ecology 14: 1377–1390

Baums IB, Johnson ME, Devlin-Durante MK, Miller MW (2010) Host population genetic structure and zooxanthellae diversity of two reef-building coral species along the Florida reef tract and wider Caribbean. Coral Reefs 29: 835–842

Bowden-Kerby A (2001) Low-tech coral reef restoration methods modeled after natural fragmentation processes. Bulletin of Marine Science 69:915–931

Bruckner AW, Hourigan TF (2000) Proactive management for conservation of *Acropora cervicornis* and *Acropora palmata*: application of the U.S. Endangered Species Act. Pages 23–27. In: Moosa, MK, Soemodihardjo S, Soegiarto A, Romimohtarto K, Nontji A, Soekarno, Suharsono (eds). Proceedings of the 9th International Coral Reef Symposium, Bali, Indonesia

Burman S, Aronson RB, van Woesik R (2012) Homogenization of coral assemblages along the Florida reef tract. Marine Ecology Progress Series 467:89–96

D'Antonio NL, Gilliam DS, Walker BK (2016) Investigating the spatial distribution and effects of nearshore topography on *Acropora cervicornis* abundance in Southeast Florida. PeerJ 4:e2473

De Marchis H (2017) The effects of ocean warming and sedimentation on the survival and growth of *Acropora cervicornis* and differential prevalence of chimerism during embryogenesis in corals. Master's Thesis, Nova Southeastern University, Fort Lauderdale, U.S.A

Done TJ (1983) Coral zonation: its nature and significance. Pages 107–147. In: Barnes DJ (ed) Perspectives on coral reefs. Australian Institute of Marine Science, Townsville, Australia

Drury C, Manzello D, Lirman D (2017) Genotype and local environment dynamically influence growth, disturbance response and survivorship in the threatened coral, *Acropora cervicornis*. PLoS One 12:1–21

Drury C, Greer JB, Baums I, Gintert B, Lirman D (2019) Clonal diversity impacts coral cover in *Acropora cervicornis* thickets: potential relationships between density, growth, and polymorphisms. Ecology and Evolution 9: 4518–4531

Edwards A, Gomez E (2007) Reef restoration concepts and guidelines: making sensible management choices in the face of uncertainty. The Coral Reef Targeted Research & Capacity Building for Management Programme/- Coral Reef Targeted Research: The University of Queensland, Australia

Gabry J, Simpson D, Vehtari A, Betancourt M, Gelman A (2019) Visualization in Bayesian workflow. Journal of the Royal Society Series A 182:1–14

Gardner TA, Côte´ IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958–960

Gelman A, Loken E (2014) The statistical crisis in science. American Scientist 102:460–465

Ginsburg RN, Shinn EA (1995) Preferential distribution of reefs in the Florida reef tract: the past is the key to the present. Oceanographic Literature Review 8:674

Goergen EA, Gilliam DS (2018) Outplanting technique, host genotype, and site affect the initial success of outplanted *Acropora cervicornis*. PeerJ 6:1–20

Goergen EA, Moulding AL, Walker BK, Gilliam DS (2019) Identifying causes of temporal changes in *Acropora cervicornis* populations and the potential for recovery. Frontiers in Marine Science 6:1–13

Goldberg WM (1973) The ecology of the coral-octocoral communities off the Southeast Florida coast: geomorphology, species composition and zonation. Bulletin of Marine Science 23:465–488

Herlan J, Lirman D (2008) Development of a coral nursery program for the threatened coral *Acropora cervicornis* in Florida. Pages 1244–1247. In: Riegl B, Dodge R (eds) Proceedings of the 11th International Coral Reef Symposium, U.S.A

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, et al. (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

Hughes TP, Ayre DJ, Connell JH (1992) The evolutionary ecology of corals. Trends in Ecology & Evolution 7:292–295

Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Velland M (2008) Ecological consequences of genetic diversity. Ecology Letters 11:609–623

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, et al. (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83

IUCN (2020) The IUCN Red List of Threatened Species. Version 2020-1. https://www.iucnredlist.org (accessed 2 Feb 2020)

Johnson ME, Lustic C, Bartels E, Baums IB, Gilliam DS, 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, Virginia

Lirman D, Fong P (1996) Sequential storms cause zone-specific damage on a reef in the northern Florida reef tract: evidence from hurricane Andrew and the 1993 storm of the century. Florida Scientist 59:50–64

Lirman D, Schopmeyer S, Galvan V, Drury C, Baker AC, Baums IB (2014) Growth dynamics of the threatened Caribbean staghorn coral *Acropora cervicornis*: influence of host genotype, symbiont identity, colony size, and environmental setting. PLoS One 9:1–9

Lohr KE, Ripple K, Patterson JT (2020) Differential disturbance effects and phenotypic plasticity among outplanted corals at patch and fore reef sites. Journal for Nature Conservation 55:125827

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. Ecology Letters 4:122–131

Manzello DP (2015) Rapid recent warming of coral reefs in the Florida Keys. Scientific Reports 5:16762

Marszalek DS, Babashoff Jr G, Noel MR, Worley DR (1977) Reef distribution in south Florida 2. Pages 223–230. In: Taylor DL (ed.). Proceedings of 3rd International Coral Reef Symposium, U.S.A

Muller EM, Bartels E, Baums IB (2018) Bleaching causes loss of disease resistance within the threatened coral species *Acropora cervicornis*. eLife 7: e35066

Nakamura T, van Woesik R (2001) Differential survival of corals during the 1998-bleaching event is partially explained by water-flow rates and passive diffusion. Marine Ecology Progress Series 212:301–304

National Marine Fisheries Service (2006) Pages 26852–26872. Endangered and threatened species: final listing determinations for Elkhorn coral and staghorn coral, 71(FR26852). National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA), St. Petersburg, FL

van Oppen MJH, Oliver JK, Putnam HM, Gates RD (2015) Building coral reef resilience through assisted evolution. PNAS 112:2307–2313

Patterson MR (1992) A mass transfer explanation of metabolic scaling relations in some aquatic invertebrates and algae. Science 255:1421–1423

Porter JW, Meier OW (1992) Quantification of loss and change in Floridian reef coral populations. American Zoologist 32:625–640

Precht WF, Miller SL (2007) Ecological Shifts along the Florida reef tract: the past as a key to the future. Pages 442. In: Aronson RB (ed) Geological approaches to coral reef ecology. Springer, New York

Precht WF, Gintert BE, Robbart ML, Fura R, van Woesik R (2016) Unprecedented disease-related coral mortality in southeastern Florida. Scientific Reports 6:31374

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/ (accessed 11 April 2020)

Ruzicka R, Colella M, Porter J, Morrison J, Kidney J, Brinkhuis V, et al. (2013) Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. Marine Ecology Progress Series 489:125–141

Schopmeyer SA, Lirman D, Bartels E, Bryne J, Gilliam DS, Hunt J, et al. (2012) In situ coral nurseries serve as genetic repositories for coral reef restoration after an extreme cold-water event. Restoration Ecology 20:696–703

Sebens KP, Miles JS (1988) Sweeper tentacles in a gorgonian octocoral: morphological modifications for interference competition. The Biological Bulletin 175:378–387

Toth LT, van Woesik R, Smith SR, Murdoch TJT, Ogden JC, Precht WF, Aronson RB (2014) Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary. Coral Reefs 33:565–577

Toth LT, Kuffner IB, Stathakopoulos A, Shinn EA (2018) A 3,000-year lag between the geological and ecological shutdown of Florida's coral reefs. Global Change Biology 24:5471–5483

Vaughan TW (1919) Pages 189–275. Corals and the formation of coral reefs. Annual Report Smithsonian Institution 1917, Washington, DC

Vollmer SV, Kline DI (2008) Natural disease resistance in threatened staghorn corals. PLoS One 3:e3718

Walton CJ, Hayes NK, Gilliam DS (2018) Impacts of a regional, multi-year, multi-species coral disease outbreak in Southeast Florida. Frontiers in Marine Science 5:323

Ware M, Garfield EN, Nedimyer K, Levy J, Kaufman L, Precht W, Winters RS, Miller SL (2020) Survivorship and growth in staghorn coral (*Acropora cervicornis*) outplanting projects in the Florida Keys National Marine Sanctuary. PLoS One 15:e0231817

van Woesik R, Jordán-Garza AG (2011) Coral populations in a rapidly changing environment. Journal of Experimental Marine Biology and Ecology 408:11–20

van Woesik R, McCaffrey KR (2017) Repeated thermal stress, shading, and directional selection in the Florida reef tract. Frontiers in Marine Science 4:1–9

van Woesik R, Irikawa A, Anzai R, Nakamura T (2012) Effects of coral-colony morphologies on mass transfer and susceptibility to thermal stress. Coral Reefs 31:633–639

van Woesik R, Ripple K, Miller S (2017) Macroalgae reduces survival of nursery-reared corals in the Florida reef tract. Restoration Ecology 26:563–569

van Woesik R, Roth LM, Brown EJ, McCaffrey KR, Roth JR (2020) Niche space of corals along the Florida reef tract. PLoS One 15:e0231104

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. Bulletin of Marine Science 88:1075–1098

Zhou H, Hanson T, Zhang J (2018) spBayesSurv: Fitting Bayesian spatial survival models using R. Journal of Statistical Software, 92. http://arxiv.org/abs/1705.04584 (accessed 11 April 2020)

Supporting Information

The following information may be found in the online version of this article:

Supplementary document.
Supplement S1. Extended methods.
Table S1. The number of coral nursery outplants per year, of the 22,634 outplanted *Acropora cervicornis* colonies used in this study, from each of six coral restoration agencies along the Florida reef tract from 2012 to 2018.
Figure S1. The number of outplanted *Acropora cervicornis* colonies along the Florida reef tract between 2012 and 2018 for each agency.
Figure S2. The number of outplanted *Acropora cervicornis* colonies along the Florida reef tract between 2012 and 2018 for each month.
Figure S3. The number of outplanted *Acropora cervicornis* colonies along the Florida reef tract between 2012 and 2018 for each of six reef habitats.
Figure S4. The number of outplanted *Acropora cervicornis* colonies along the Florida reef tract between 2012 and 2018 for each of seven geographical subregions.
Figure S5. The number and size of outplanted *Acropora cervicornis* colonies along the Florida reef tract for each agency.
Figure S6. Survival of three size classes of *Acropora cervicornis* colony outplants for fore-reef habitats in the Broward–Miami subregion, in 2016.
Figure S7. Survival of three size classes of *Acropora cervicornis* colony outplants for fore-reef habitats in the Biscayne subregion, in 2016.
Figure S8. Survival of sizes of *Acropora cervicornis* outplants for fore-reef habitats in the upper Florida Keys subregion, in 2016.
Figure S9. Survival of sizes of *Acropora cervicornis* outplants for fore-reef habitats in the middle Florida Keys subregion, in 2016.
Figure S10. Survival of sizes of *Acropora cervicornis* outplants for fore-reef habitats in the Marquesas subregion, in 2016.
Figure S11. Survival of sizes of *Acropora cervicornis* outplants for fore-reef habitats in the Dry Tortugas subregion, in 2016.
Figure S12. Survival of *Acropora cervicornis* outplants in six different habitats for colonies between 16 and 50 cm in the Broward–Miami subregion, in 2016.
Figure S13. Survival of *Acropora cervicornis* outplants in six different habitats for colonies between 16 and 50 cm in the Biscayne subregion, in 2016.
Figure S14. Survival of *Acropora cervicornis* outplants in six different habitats for colonies between 16 and 50 cm in the upper Florida Keys subregion, in 2016.
Figure S15. Survival of *Acropora cervicornis* outplants in six different habitats for colonies between 16 and 50 cm in the middle Florida Keys subregion, in 2016.
Figure S16. Survival of *Acropora cervicornis* outplants in six different habitats for colonies between 16 and 50 cm in the Marquesas subregion, in 2016.
Figure S17. Survival of *Acropora cervicornis* outplants in six different habitats for colonies between 16 and 50 cm in the Dry Tortugas subregion, in 2016.

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