1 Assessment of wild and restored staghorn coral *Acropora cervicornis* across three reef
2 zones in the Cayman Islands

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16 Abstract

17 Interest in restoring staghorn coral *Acropora cervicornis* has grown following the
18 widespread decline of this species in recent decades. To date, thousands of nursery-reared
19 *A. cervicornis* have been outplanted to restore degraded reefs, but survivorship and growth
20 among outplanted colonies can be spatially variable. In particular, data on distribution of
21 remnant wild populations and outplant performance in varying reef zones is lacking. To
22 address this gap, we conducted a study to characterize existing wild populations and assess
23 performance of nursery-reared, outplanted *A. cervicornis* among three reef zones of varying
24 depth at Little Cayman Island: the shallow back reef (0-3 m), the intermediate spur-and-
25 groove reef (8-15 m), and the deep reef terrace (>15 m). Wild populations of *A. cervicornis*
26 were present in each reef zone, and colony height and prevalence of predation by *Stegastes*
27 spp. were highest in the intermediate zone. For outplanted *A. cervicornis*, survivorship
28 differed among sites and was lowest for outplants in the deep zone during the 85-day
29 observation period. Post-outplant growth and branching was lowest among outplants in the
30 shallow zone due to high rates of colony breakage. Following the conclusion of the study, a
31 mortality event occurred in which 90% of outplants at the shallow plots died during a
32 period of elevated sea temperature. The information provided in this study suggests that
33 intermediate spur-and-groove reefs are optimal for outplanting activities in Little Cayman
34 using existing restoration methods. These data could be useful for coral restoration
35 practitioners and government agencies in the Caribbean, particularly the Cayman Islands,
36 which is actively expanding its coral nursery program. New strategies must be developed
37 to improve restoration outcomes in shallow and deep zones.

38 Key Words: coral, restoration, endangered species, conservation, Caribbean Sea, Cayman
39 Islands

1. Introduction

Staghorn coral *Acropora cervicornis* is a fast-growing, branching species that historically occurred across a wide range of depths (i.e. 1-25 m, Aronson et al., 2008) and reef types (i.e. forereef, backreef, and lagoonal habitats, Aronson and Precht, 2001) in the Caribbean. *A. cervicornis* is critical for building three-dimensional structure on reefs, creating habitat for reef-dwelling species (Bellwood et al., 2004; Nyström, 2006; Young et al., 2012) and providing shoreline protection (Ferrario et al., 2014). Though once spatially dominant in the Caribbean (Pandolfi and Jackson, 2006), this species has declined throughout its range and is now designated as critically endangered by the International Union for Conservation of Nature (Aronson et al., 2008). Combinations of stressors including disease (Gladfelter, 1982), temperature stress (Lesser et al., 2007), pollution (Bak, 1987), and hurricanes (Woodley et al., 1981) have led to the decline of *A. cervicornis*. Remnant populations of *A. cervicornis* generally persist at low abundances throughout the Caribbean (Aronson et al., 2008), but natural recovery has been limited due to low rates of sexual reproduction combined with Allee effects (Aronson and Precht, 2001).

To mitigate this decline, coral gardening has been widely adopted to grow new colonies via asexually propagating portions of healthy, wild colonies (Bowden-Kerby, 2001; Rinkevich, 1995). The primary goal of coral gardening is to create a self-sustaining stock of maricultured coral within a nursery, which can later be transplanted to restore degraded reefs (Epstein et al., 2003, 2001; Rinkevich, 1995; Young et al., 2012).

Transplantation from nurseries to reefs, known as outplanting, immediately increases reef

complexity and local abundance of *A. cervicornis* at the outplanted site. In addition, *A. cervicornis* is typically outplanted in multi-genotype clusters, thereby creating opportunities for future sexual reproduction, which can increase genetic diversity and enhance natural recovery of the species (M. E. Johnson et al., 2011). Thousands of *A. cervicornis* colonies from dozens of nurseries have been outplanted throughout the Caribbean (Young et al., 2012).

Best practices for outplanting nursery-reared *A. cervicornis* recommend selecting sites with factors including, but not limited to, suitable water quality, solid substrate, and the presence of wild *A. cervicornis* (M. E. Johnson et al., 2011). Following region-wide declines, *A. cervicornis* was completely extirpated from some reefs (Aronson and Precht, 2001). Due to multiple stressors, some reefs have also transitioned from a coral-dominated state to a macroalgal-dominated state, which can inhibit coral settlement, growth, and survival (Fung et al., 2011; Hughes, 1994). For this reason, systems that have been severely degraded and transitioned to an alternative state may be unsuitable for restoration of formerly-present species (Suding et al., 2004). Therefore, the presence of remnant wild *A. cervicornis* in a target region provides evidence that local conditions are suitable for restoration (M. E. Johnson et al., 2011).

Recent efforts have integrated field observations, satellite data, and modelling to prioritize sites for Caribbean *Acropora* re-establishment on the scale of km² (Wirt et al., 2015). However, selection of outplanting sites within and among reefs with conditions suitable for restoration can still be subjective, and the fate of outplanted colonies may vary among sites. For example, in a study from Belize, outplant survivorship after one month

84 ranged from 38–97% between plots at the same location (Bowden-Kerby and Carne, 2012).
85 Similar variability in survivorship among adjacent outplant plots has been observed in the
86 Cayman Islands (Lohr unpublished data). However, in Puerto Rico, no difference in
87 survivorship was reported between two plots of outplanted *A. cervicornis* at similar sites
88 several km apart, although differences in growth were found (Mercado-Molina et al., 2015).
89 In addition to understanding how outplant performance varies among sites, it is critical to
90 characterize differences in restoration outcomes among diverse reef zones. Prior
91 outplanting studies have investigated sites with depths ranging from 1 m (Bowden-Kerby
92 and Carne, 2012) to 12 m (Hollarsmith et al., 2012). Shallow reefs in particular have been
93 identified as important targets for coral restoration because of their ability to reduce wave
94 energy (Ferrario et al., 2014). Although *A. cervicornis* occurs in shallow reef zones such as
95 backreefs, it was historically dominant in deeper forereef habitats (e.g. Goreau, 1959;
96 Logan, 2013). It is therefore important to develop the ability to restore *A. cervicornis* in
97 each zone where it occurs.

98 Despite the need to restore *A. cervicornis* across a diverse range of site types, the
99 extent to which a single nursery may be used to conduct restoration among sites at varying
100 reef zones has received little attention. Best practice guides recommend collecting, rearing,
101 and outplanting coral at similar depths (Edwards and Gomez, 2007; Johnson et al., 2011),
102 however the authors are unaware of a study which has systematically investigated the
103 outcomes of, and potential limitations for, conducting restoration among reef zones of
104 varying depth. Previous outplanting studies of *A. cervicornis* have compared outplant
105 performance among similar sites of depths within a range of no more than ~3m (e.g.

Bowden-Kerby and Carne, 2012; Hollarsmith et al., 2012; Mercado-Molina et al., 2015). However, corals are capable of acclimating to new environments, including a variety of temperature (Mayfield et al., 2012; Palumbi et al., 2014) and light (Titlyanov et al., 2001) regimes, as well as high- and low-energy sites (Smith et al., 2007). Therefore, it is possible that *A. cervicornis* outplants sourced from a single nursery location would be able to acclimate to multiple types of outplant sites.

Scientists, resource managers, and governments are interested in better understanding the outcome of *A. cervicornis* restoration efforts in diverse reef zones. For example, the Cayman Islands government is in the process of expanding its coral nursery program to multiple locations nationwide, and information on outplant success among reef zones may be of interest. Reefs in the Cayman Islands consist of a deep wall system with well-defined zonation by depth (Fig. 1, Logan, 2013, 1994). Developing the ability to effectively enhance *A. cervicornis* populations in each of these zones is a critical next step for restoration programs in the Cayman Islands, and could also have relevance to other Caribbean sites with distinct reef zonation.

As a first step in addressing this issue, we conducted a study to test growth and survivorship among outplants within three reef zones at Little Cayman, Cayman Islands: the shallow back reef (0-3 m), the intermediate spur-and-groove reef (8-15 m), and the deep reef terrace (>15 m) (Fig. 1, 2). Outplants in this study were sourced from an existing *A. cervicornis* nursery at Little Cayman, which was established in 2012 at a depth ranging from 4 to 7 m (see Lohr et al., 2015). To determine the suitability of each zone for *A. cervicornis* restoration activities, we simultaneously surveyed and characterized the extant

wild population in each zone. Recent surveys of Little Cayman reefs have not described the extant distribution of *A. cervicornis* (e.g. Manfrino et al., 2013), however anecdotal evidence and previously published data suggest this species occurs in both the shallow back reef and deeper spur-and-groove reefs in the Cayman Islands (Manfrino et al., 2003). We tested two hypotheses: (1) Wild *A. cervicornis* will be present in each of the three reef zones studied, and the condition (in terms of predation and disease prevalence) of each population will be similar, (2) Outplanted *A. cervicornis* will not differ in growth, survivorship, or condition (predation, disease prevalence, and post-outplant breakage) among reef zones. Information provided in this study could be used to inform future *A. cervicornis* restoration efforts in the Cayman Islands and the wider Caribbean.

2. Methods

2.1 Wild Population Surveys

Surveys were conducted throughout the western half of Little Cayman between June and August 2015 to determine the extent and condition of wild *Acropora cervicornis* populations within each coral-dominated reef zone (i.e. shallow backreef (0-3 m), intermediate spur-and-groove reef (8-15 m), and deep reef terrace (>15 m)). For the purposes of this study, these reef zones will be identified as shallow, intermediate, and deep, respectively. Given that *A. cervicornis* is sparse on Little Cayman reefs (Manfrino et al., 2003), surveys were conducted using the roving diver method (modified from Schmitt et al., 2002). Shallow zone surveys were completed on snorkel, while intermediate and deep zone surveys were done using SCUBA. Approximately five hours of search time was applied in each reef zone.

Upon locating an *A. cervicornis* colony, site depth was recorded and the colony's maximum diameter and height were measured using a PVC meter-stick marked with 10 cm increments. Occurrence of predation was determined for each colony by identifying and recording the presence or absence of predation scars following Miller et al. (2014a; the gastropod *Coralliphila abbreviata*), Miller et al. (2014b; the fireworm *Hermodice carunculata*), and Schopmeyer and Lirman (2015; farming damselfish, *Stegastes* spp.). Occurrence of disease was determined for each colony by identifying and recording the presence or absence of disease signs following Miller et al. (2014a). Prevalence was then calculated for each type of predation and for disease as the percent of the total population affected by each condition.

2.2 Outplanting Experiment

A. cervicornis colonies grown in the Little Cayman nursery were outplanted in May 2015. Outplanted colonies were clipped from established colonies that had been propagated within the nursery since 2012. A total of 60 outplants ranging in size from 11 to 33 cm total linear extension (TLE, Lirman et al., 2014; mean $\pm$ SE = 19.57 ± 0.75) were utilized for the study and were randomized across treatments. Four unique genotypes identified in the Little Cayman nursery in 2014 via genotyping-by sequencing (C. Drury, University of Miami/RSMAS, unpublished data) were used for this study. Of the 60 colonies clipped for outplanting, 24 colonies were sourced from genotype A, and 12 each were sourced from genotypes B, C, and D. Colonies were outplanted in a balanced design with respect to genotype.

Outplanting plots were selected at three distinct reef zones along a single longitudinal transect perpendicular to shore (Fig. 2). All plots were located within 200 m of the nursery site (Fig. 2), and were within the range of concurrent wild surveys. Two plots of 10 colonies each were established in the shallow, intermediate, and deep reef zones at depths of 1, 10, and 16 m, respectively. Photosynthetically active radiation (PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured at solar noon on a clear day at the nursery and at each reef zone ($n = 10$ measurements per site) using a handheld PAR meter (Apogee Instruments, USA). At each plot, masonry nails were installed into areas of bare substrate in a 1 x 4 m grid. Outplants were attached to nails using cable ties and secured to the substrate at the base of the nail using a two-part epoxy putty (M. E. Johnson et al., 2011; Lirman et al., 2014). Scaled photographs of outplanted colonies were taken at approximately 30-day intervals over the course of 85 days ($n = 4$ intervals) using a digital camera (Olympus, Japan). Condition of each colony was recorded, including signs of disease and predation, using the same methods as the wild *A. cervicornis* surveys. Broken colonies (i.e. colonies missing a portion of skeleton and tissue with an exposed skeletal lesion visible) were noted. Frequency of breakage was calculated as the percent of broken colonies per zone by the end of the experiment. The total number of branches (≥ 1 cm) was counted, and TLE of each colony was measured using ImageJ 1.43 software (National Institutes of Health, USA). Temperature was recorded continuously in situ at one plot within each reef zone using HOBO Pendant® data loggers (Onset Computer Corporation, USA).

2.4 Statistical Analysis

Statistical analysis of experimental and survey data was conducted using R statistical software version 3.1.2 (R Core Team, 2014). All statistical tests were performed at a significance level of $\alpha = 0.05$ and all means are presented as mean $\pm$ SE. Normality and homogeneity of variance were assessed using the Shapiro-Wilk test and Levene's test, respectively. Wild colony size data did not meet the assumptions of normality and homogeneity of variance, and was therefore compared among reef zones using a nonparametric Kruskal-Wallis test followed by Dunn's post-hoc test in the R package 'dunn.test' (Dinno, 2015). Chi-square tests were conducted to determine whether prevalence of disease or any type of predation differed between populations of *A. cervicornis* located in varying reef zones.

Initial outplant size data were log transformed to meet the assumptions of normality and homogeneity of variance. These data were compared among treatments using ANOVA to test for any differences in initial size of outplanted colonies among reef zones. Net growth and net change in number of branches were compared among reef zones using ANOVA with a Tukey HSD post-hoc test. Differences in colony survivorship among reef zones throughout the 85-day study were evaluated using Kaplan-Meier Survival Analysis in the R package 'survival' (Therneau, 2015). Frequency of *A. cervicornis* colony breakage and predation was analyzed among reef zones using a chi-square test.

3. Results

3.1 Wild Population Surveys

Table 1 contains summary data from wild colony surveys. Extant populations of *A. cervicornis* were observed in each reef zone surveyed in Little Cayman. Maximum diameter of wild colonies did not differ among reef zones, but differences in colony height were detected ($H = 6.57$, $df = 2$, $p < 0.05$). Dunn's post-hoc indicated that mean height of wild *A. cervicornis* was greater in the intermediate zone compared to the shallow and deep zones. Prevalence of predation by *H. carunculata* and *C. abbreviata* did not differ among reef zones. However, predation by *Stegastes* spp. differed among reef zones ($X^2 = 6.20$, $df = 2$, $p < 0.05$) and was most frequent in the intermediate zone. Disease prevalence in wild *A. cervicornis* did not differ among reef zones.

3.2 Outplanting Experiment

Mean photosynthetically active radiation was $2,403.00 \pm 120.48 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the shallow site (1 m), $1,267.10 \pm 45.64 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the nursery (6 m), $964.20 \pm 27.42 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the intermediate site (10 m), and 757.22 ± 18.61 at the deep site (16 m). Mean initial size of outplanted *A. cervicornis* colonies did not differ significantly between reef zones. Net total linear extension (TLE) differed between reef zones after 85 days ($F = 20.46$, $df = 2$, $p < 0.001$; Fig. 3) and was lowest at the shallow back reef site, where colonies experienced a mean decrease in TLE as a result of breakage (mean net TLE = -4.04 ± 1.98 cm). Increases in mean net TLE were observed at both the intermediate (11.90 ± 1.86 cm) and deep sites (7.23 ± 1.66 cm), but no statistical difference was found between these sites. Net number of branches also differed among outplanted colonies in varying reef zones ($F = 13.58$, $df = 2$, $p < 0.001$), and was lowest at the shallow site (0.00 ± 0.53)

238 compared to the intermediate (4.16 ± 0.62) and deep (2.33 ± 0.48) sites, which did not
239 differ significantly.

240 Frequency of colony breakage varied between sites ($X^2 = 13.68$, $df = 2$, $p = 0.001$),
241 and breakage was highest for the shallow back reef at a frequency of 70% (intermediate =
242 30%, deep = 15%). *C. abbreviata* predation was observed among outplanted colonies at the
243 deep site at a rate of 5% and *H. carunculata* predation was observed among outplanted
244 colonies at the intermediate site at a rate of 15%. Predation was not observed among
245 colonies in the shallow backreef, and *Stegastes* spp. predation was not observed among
246 outplanted *A. cervicornis*. No statistically significant difference existed in predation
247 prevalence between reef zones.

248 Survival patterns of outplanted *A. cervicornis* differed between reef zones during
249 the 85-day study period (Kaplan-Meier $X^2 = 14.7$, $df = 2$, $p = 0.001$), and survival was
250 lowest at the deep site. Survival was 60% at the deep site and 95% at the intermediate site
251 after 32 days, but no additional mortality was observed at either site for the remainder of
252 the study. No mortality was observed among the shallow plots during the 85-day study
253 period. However, following the conclusion of the study period, total survivorship within the
254 shallow plots dropped to 10% during a period of unusually high temperature in which mean
255 daily sea temperature exceeded 30.5°C for 20 consecutive days. However, a population of
256 wild *A. cervicornis* less than 5 m from one of the shallow outplant plots survived this
257 period of elevated temperature.

4. Discussion

Regional assessments of population trends for *A. cervicornis* suggest that populations remain depleted but stable following a sharp decline in abundance in the early 1980s (Aronson et al., 2008; Schutte et al., 2010). Our observations of small remnant populations of wild *A. cervicornis* in each coral-dominated reef zone at Little Cayman are consistent with this reported trend as well as with reports of sustained *A. cervicornis* cover at other locations in the Caribbean (Crabbe, 2014; Lidz and Zawada, 2013; Lucas and Weil, 2015). The persistence of remnant wild *A. cervicornis* populations in three major reef zones in the Cayman Islands warrants investigation of the potential for outplanting in each zone. Although the current study provides a snapshot of the extant wild *A. cervicornis* population in Little Cayman, continued monitoring of wild *A. cervicornis* is recommended to fully understand long-term, local demography of this species.

Among wild *A. cervicornis*, colony height and the prevalence of predation by *Stegastes* spp. was found to differ among reef zones, and each of these was highest in the intermediate zone. Increases in *Stegastes* predation with *A. cervicornis* colony size have been documented in Florida (Schopmeyer and Lirman, 2015), suggesting that increased height among colonies in the intermediate zone could explain observed higher rates of *Stegastes* predation in that zone. The relationship between colony size and *Stegastes* predation also indicates that this type of predation could increase among outplanted colonies as they grow larger (Schopmeyer and Lirman, 2015).

Prevalence of both predation and disease among the outplanted *A. cervicornis* population was low and did not differ among reef zones, suggesting that predation is not an

important factor in initial outplant success at Little Cayman. This finding is also supported by Griffin et al. (2015), who observed minimal predation within three months following outplanting of *A. cervicornis* in the U.S. Virgin Islands. In the same study, mean *A. cervicornis* outplant growth after three months was 9.0 ± 0.76 cm (Griffin et al., 2015), which is consistent with values observed at the intermediate and deep sites in the present study. Griffin et al. (2015) also reported 98% survivorship of outplants after three months, which is similar to our observations of high survivorship in both the intermediate and shallow sites during the study period.

In contrast, long-term studies report somewhat lower survivorship among outplanted *A. cervicornis* after one year (e.g. 61.2 – 65.9% in Puerto Rico, Mercado-Molina et al., 2015; $89.5 \pm 2.4\%$ in Florida, Schopmeyer and Lirman, 2015), suggesting that time post-outplant could be a factor in survivorship. Our observations of high mortality in the shallow zone following the conclusion of the three-month study period suggest that long-term monitoring (i.e. ≥ 1 year) would be valuable to assess restoration outcomes.

Ultimately, high mortality at the shallow plots immediately after the conclusion of the study as well as at the deep plots within the first month of study suggest that these zones may be unsuitable for outplanting using current restoration strategies. However, high rates of growth and branching at the intermediate site suggest that current *A. cervicornis* restoration methods in the Cayman Islands may be best suited to this zone. In *A. cervicornis*, high rates of growth are a primary indicator of health (Lirman et al., 2014), suggesting that colonies planted to the intermediate zone remained robust throughout the study. Importantly, high growth rates, branching, and survivorship among outplants in the intermediate zone could

increase availability and complexity of habitat for other reef fauna relative to other zones. Increased cover of complex branching corals has been linked to increases in abundance and species richness of reef fishes (Holbrook et al., 2008, 2002; M. K. Johnson et al., 2011).

Our data ultimately suggest that a single nursery may be ineffective for rearing outplants which can be used to restore the shallow and deep zones at Little Cayman. Growth and branching patterns among outplanted *A. cervicornis* in the shallow zone were predominantly influenced by colony breakage. Avoidance of nursery and outplant sites characterized by high wave energy has been proposed as a strategy to avoid breakage (M. E. Johnson et al., 2011; Young et al., 2012), however *A. cervicornis* is known to be capable of persisting at sites with high wave energy (Bottjer, 1980), including at Little Cayman as documented by this study. In addition, although no visible bleaching was observed during the study period, temperature stress was likely a factor in the shallow zone mortality event immediately following the conclusion of the study. Daily mean temperature exceeded 30.5°C, one degree greater than the maximum monthly mean temperature reported for Little Cayman (i.e. 29.5°C, van Hooidonk et al., 2012), for a period of nearly three weeks. Corals have been shown to experience considerable thermal stress when this threshold is exceeded (Glynn and D'Croz, 1990; Logan et al., 2012). Additionally, temperatures tend to have higher ranges in shallow reef habitats compared to the outer reef (Craig et al., 2001), and branching corals are known to have relatively high sensitivity to warming events (Baird and Marshall, 2002; Brown and Suharsono, 1990; Gates and Edmunds, 1999; Loya et al., 2001). It is therefore logical to conclude that *A. cervicornis* colonies in the shallow plots would have been negatively affected by extreme high temperatures after a relatively short

acclimation period of ~3 months. Colony breakage may have compounded the negative effects of the warming event by allocating colony resources to repair damage, which can in some cases increase the likelihood of mortality (Hall, 2001). Unlike at the shallow site, all mortality at the deep site occurred within the first month following outplanting. Reduced PAR is known to decrease calcification and linear extension (Chalker and Taylor, 1975; Enochs et al., 2014; Kendall et al., 1985) and can cause mortality of *A. cervicornis* (Rogers, 1979). This environmental variable could therefore be a factor in the poorer performance of colonies at the deep site. Ultimately, we lack the data necessary to fully understand the cause of mortality among deep outplants.

This work represents a case study of initial *A. cervicornis* outplant performance across three diverse reef zones where wild colonies persist, however we acknowledge limitations to our study as well as remaining questions that could be addressed in future investigations. First, our study was constrained by low sample size due to colony availability within the nursery, and therefore our results must be interpreted carefully. We recommend repeating this study with a larger number of corals and over a longer time scale to better understand reef zone-specific differences in outplant performance. Despite limitations, these data have value in guiding future outplant site selection, and will likely be particularly useful for practitioners in the Cayman Islands and other Caribbean sites with similar reef zonation. Additionally, new strategies should be tested to attempt to improve outplant performance in the shallow and deep zones. In particular, the effect of nursery donor colony site of origin could be explored, as site of origin has been shown to influence colony performance in reciprocal transplantation experiments (Raymundo, 2001). The

effect of nursery location should also be considered and could be tested by establishing nurseries within each target outplanting zone and conducting reciprocal outplanting. Colony performance was overall best in the zone with characteristics most similar to the nursery (i.e. the intermediate zone; Fig. 1), a result that tentatively supports the recommendations of M. E. Johnson et al. (2011), who suggest outplanting at depths similar to those of the nursery site. Finally, strategies to reduce breakage could be developed and tested to improve outplant performance at sites with high wave energy. For example, anecdotal evidence suggests that adding three points of contact between the colony and the substrate could increase stability of outplanted *A. cervicornis* (K. Ripple, Coral Restoration Foundation, personal communication) compared to the single point of contact method used in this study. The relative difference in colony breakage between outplant methods has yet to be directly evaluated.

This study reports characteristics of the extant wild *A. cervicornis* population at Little Cayman, a site with minimal direct anthropogenic impact and healthy reefs relative to other Caribbean locations (Manfrino et al., 2013). In addition, a concurrent assessment of the effect of reef zonation by depth on growth and survivorship was performed among nursery-reared staghorn coral. These results suggest that outplanting efforts currently have the most initial success in the intermediate spur-and-groove reef zone. This information can be used to inform site selection for future outplanting activities in the Cayman Islands and potentially at sites with similar nursery practices and reef zonation. Additional studies should be conducted to better understand the effect of site selection on outplant performance. New techniques must also be developed to improve the outcomes of *A.*

cervicornis restoration activities in the shallow back reef and deep reef terrace in order to extend the ecological services provided by coral restoration to these zones.

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Table 1 Characteristics of extant wild colonies. Asterisks (*) in headings indicate that significant differences within that factor were present among reef zones. Letters on values denote differences among reef zones per Dunn's post-hoc test.

Reef Zone	Number of colonies located	Mean Depth (m) $\pm$ SE	Mean Max Diameter (cm) $\pm$ SE	Mean Height (cm) $\pm$ SE (*)	<i>H. carunculata</i> Predation Prevalence	<i>C. abbreviata</i> Predation Prevalence	<i>Stegastes</i> Predation Prevalence (*)	Disease prevalence
Shallow Back Reef	16	0.74 $\pm$ 0.10	61.25 $\pm$ 6.73 ^a	31.13 $\pm$ 2.53 ^a	25.00%	50.00%	6.25%	0%
Intermediate Spur-and-Groove Reef	16	10.93 $\pm$ 0.26	89.38 $\pm$ 14.68 ^a	63.81 $\pm$ 13.95 ^b	25.00%	43.75%	43.75%	12.5%
Deep Reef Terrace	44	16.00 $\pm$ 0.42	74.73 $\pm$ 8.11 ^a	44.66 $\pm$ 5.67 ^a	23.26%	27.91%	23.26%	11.36%

Figure Captions

Figure 1 Zonation by depth in Little Cayman, modified from Logan (1994). Three major coral-dominated reef zones are present, including (A) the shallow back reef (i.e. shallow), (B) the intermediate spur-and-groove reef (i.e. intermediate), and (C) the deep reef terrace (i.e. deep). Wild *Acropora cervicornis* surveys and the *A. cervicornis* outplanting experiment occurred in each of zones A, B, and C.

Figure 2 Outplant experiment location in context of the Caribbean region, with points indicating the location of the nursery and each study site. All outplant sites were within 250 m of the nursery location along an approximately longitudinal transect perpendicular to shore. Aberrations from this transect were due to variation in availability of suitable hard substrate for outplanting.

Figure 3 Total linear extension (TLE) of outplanted *Acropora cervicornis* in each reef zone over time. Error bars represent SE. No significant difference in initial size of outplanted *A. cervicornis* was detected among zones at beginning of the experiment. Colonies at the shallow site experienced a decrease in mean TLE over time due to high rates of natural breakage, while TLE increased at both the deep and intermediate sites over time. Net TLE was significantly lower at the shallow site compared to both the intermediate and deep sites on day 85 ($F = 20.46$, $df = 2$, $p < 0.001$).

Figure 2

Figure 3