Coral Reefs
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REPORT

Regional restoration benchmarks for *Acropora cervicornis*

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Abstract Coral gardening plays an important role in the recovery of depleted populations of threatened *Acropora cervicornis* in the Caribbean. Over the past decade, high survival coupled with fast growth of in situ nursery corals have allowed practitioners to create healthy and genotypically diverse nursery stocks. Currently, thousands of corals are propagated and outplanted onto degraded reefs on a yearly basis, representing a substantial increase in the abundance, biomass, and overall footprint of *A. cervicornis*. Here, we combined an extensive dataset collected by restoration practitioners to document early (1–2 yr) restoration success metrics in Florida and Puerto Rico, USA. By reporting region-specific data on the impacts of fragment collection on donor colonies, survivorship and productivity of nursery corals, and survivorship and productivity of outplanted corals during normal conditions, we provide the basis for a stop-light indicator framework for new or existing restoration programs to evaluate their performance. We show that current restoration methods are very effective, that no excess damage is caused to donor colonies, and that once outplanted, corals behave just as wild colonies. We also provide science-based benchmarks that can be used by programs to evaluate successes and challenges of their efforts, and to make modifications where needed. We propose that up to 10% of the biomass can be collected from healthy, large *A. cervicornis* donor colonies for nursery propagation. We also propose the following benchmarks for the first year of activities for *A. cervicornis* restoration: (1) >75% live tissue cover on donor colonies; (2) >80% survivorship of nursery corals; and (3) >70% survivorship of outplanted corals. Finally, we report productivity means of 4.4 cm yr^{-1} for nursery corals and 4.8 cm yr^{-1} for outplants as a frame of reference for ranking performance within programs. Such benchmarks, and potential subsequent adaptive actions, are needed to fully assess the long-term success of coral restoration and species recovery programs.

Keywords *Acropora cervicornis* · Restoration · Species recovery · Survival · Productivity · Growth

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Introduction

In the last 20 yr, active restoration to mitigate declines in coral cover has increased worldwide and coral propagation for restoration is now considered an essential component of

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coral conservation and management plans (Rinkevich 2005; Precht 2006; Edwards and Gomez 2007; Lirman and Schopmeyer 2016). In 2012, over 60 restoration projects focusing on the threatened coral genus *Acropora* were identified in the Caribbean (Young et al. 2012). Once one of the Caribbean's predominant reef-building coral genera, *Acropora* has suffered significant degradation from both biological and anthropogenic stressors (Jaap et al. 1988; Porter and Meier 1992) and is now listed as threatened under the Endangered Species Act (NMFS 2006, 2014). The decline of acroporids leads to the loss of reef function and structural complexity, both of which are critical for reef growth, fisheries habitat, coastal protection, and overall reef biodiversity (Bruckner 2002; Alvarez-Filip et al. 2009).

Adapted from terrestrial silviculture, "coral gardening" is one of the most commonly used coral propagation and restoration methods (Rinkevich 1995; Bowden-Kerby 2001; Epstein et al. 2003; Shafir et al. 2006; Shafir and Rinkevich 2008; Shaish et al. 2008). This method involves removing a limited amount of tissue and skeleton (from a few polyps to small branches) from healthy wild coral populations and propagating an initial stock within ex situ or, more commonly, in situ coral nurseries. Throughout the Caribbean, in situ coral nurseries are used to propagate a renewable source of the threatened staghorn coral, *Acropora cervicornis* for restoration and species recovery (Johnson et al. 2011). Nursery-reared corals are "outplanted" from nurseries to reef restoration sites to bridge spatial gaps between existing populations (Griffin et al. 2012, 2015), enhance *A. cervicornis* abundance, supplement genetic and genotypic diversity (Lirman and Schopmeyer 2016), and promote natural recovery through the creation of sexually reproductive populations (Baums 2008). *Acropora cervicornis* is considered a good candidate for use in restoration projects due to its high growth rates, natural use of fragmentation for asexual reproduction, ability to heal wounds, and high survivorship of fragments compared to other coral species (Gladfelter et al. 1978; Tunnicliffe 1981; Bak and Criens 1982; Highsmith 1982; Lirman et al. 2010, 2014a).

The ability of coral propagation and restoration programs to create renewable sources of corals for use in restoration using low-cost, science-based methods has been well documented (Soong and Chen 2003; Lirman et al. 2010, 2014a; Rinkevich 2014). While long-term monitoring is required by permitting agencies for many, if not all, restoration projects, few studies have published the impacts of collection on existing wild populations used to populate coral nurseries (Epstein et al. 2001; Shafir et al. 2006; Lirman et al. 2010), or the success of restoration projects over the course of more than a few months (Bruckner and Bruckner 2001; Griffin et al. 2015) especially in the Caribbean where coral gardening activities generally began more recently than in the Red Sea and the Pacific. This information is needed to evaluate the performance of restoration efforts. These knowledge gaps within the literature can lead to criticism of restoration or population enhancement programs and questions the ability of such programs to successfully create functioning populations (Rinkevich 2014). In this study, we address these gaps by evaluating the effects of fragment collection on donor colonies, documenting the success of coral propagation within in situ coral nurseries, and tracking the survival and productivity of nursery-reared corals for up to 2 yr after outplanting in Florida and Puerto Rico, USA. Based on our analyses, which combine information from thousands of staghorn corals during "normal" conditions (i.e., no disease or thermal stress) from >120 distinct genotypes from six geographical regions, we propose coral propagation and outplanting benchmarks that may be used by existing and new restoration programs to assess performance and progress towards restoration goals.

Materials and methods

Beginning in 2009, funding was received as part of the American Recovery and Reinvestment Act (National Oceanic and Atmospheric Administration, NOAA) for the creation or expansion of *Acropora* species recovery programs along the Florida Reef Tract and in Puerto Rico. In-water coral nurseries were installed or expanded by a partnership of state and federal government agencies, non-profit organizations, and universities, thus creating the largest coordinated species recovery effort in the world (Table 1). To populate each local nursery, partners collected only small branches or branch tips equaling <10% of the total colony size (Epstein et al. 2001) from healthy, wild (donor) *A. cervicornis* colonies using hand cutters, or collected corals of opportunity (i.e., corals found detached from the reef). Donor colonies were monitored for at least 12 months post collection to determine impacts of fragment collection. The coral genotypes of the donor colonies were identified by the Baums Lab (Penn State University) using microsatellite markers as described by Baums et al. (2009). Collected branches or colonies were fragmented to create smaller fragments and were secured to propagation platforms, including cement blocks (Florida nurseries only) and floating underwater coral arrays (FUCAs; Puerto Rico only) (described in detail in Johnson et al. 2011). Coral nurseries were maintained (monthly to quarterly) to remove coral competitors including macroalgae, hydroids, and bivalves and predators such as *Hermodice* and *Coralliophila*. Individually tagged corals were monitored for survival, growth, and condition. After allowing coral

Table 1 Program information for in situ *Acropora cervicornis* propagation nurseries and outplanting as of 2016

Program	Location	Year established	# nurseries	# genotypes	# nursery corals	# outplant sites	# outplanted corals
Nova Southeastern University	BC, FL	2007	3	30	3376	18	5467
University of Miami	MIA, FL	2007	3	36	3240	33	6818
Florida Fish and Wildlife Conservation Commission	MK, FL	2009	2	27	1900	11	2682
Mote Marine Laboratory	LK, FL	2007	2	38	>8000	29	7260
The Nature Conservancy	DRTO, FL	2010	1	15	1500	4	4100
National Oceanic and Atmospheric Administration	PR	2008	2	15	2300	25	10,180
		Total	13	161	20,316	120	36,507

A subset of these corals were monitored by each partner for this study

BC Broward County, FL, *MIA* Miami-Dade County, FL, *UK* Upper Keys, FL, *MK* Middle Keys, FL, *LK* Lower Keys, FL, *DRTO* Dry Tortugas National Park, FL, *PR* Puerto Rico, USA

fragments to grow and create an initial stock in nurseries, corals were outplanted within each region to local reefs identified to have suitable conditions and substrate for coral survival. Corals were outplanted by securing them to the reef using nails, cable ties, and/or epoxy as described by Johnson et al. (2011). Individually tagged outplants were monitored (monthly or quarterly) for survival, condition, and growth for at least 1 yr after transplantation (2 yr in three Florida regions).

Growth and survival data were collected for both nursery corals and coral outplants by six nursery programs: Nova Southeastern University (Broward County, BC), University of Miami (Miami-Dade County, MIA), Florida Fish and Wildlife Conservation Commission (Middle Keys, MK), Mote Marine Laboratory (Lower Keys, LK), The Nature Conservancy (Dry Tortugas National Park, DRTO), and NOAA (Puerto Rico, PR). We compiled the most complete dataset possible from our partner restoration practitioners, but some data were not available for all metrics from all partners. If more than one type of propagation platform was used within a nursery, growth and productivity data were calculated separately for each platform type due to potential differences in extension rates. Nursery data were collected for at least 1 yr after corals were installed within the nurseries: BC, MIA, MK, and PR (2010–2011) and LK and DRTO (2011–2012). Outplant survival data were collected for 1 yr at multiple sites in LK and PR (2012–2013) and for 2 yr at multiple sites in BC, MIA, and MK (2012–2014). Coral growth and productivity data were collected for 1 yr following outplanting in BC, MIA, MK, and LK. Outplant data were collected in DRTO as part of a separate outplant experiment conducted during 2014–2015. Not all parameters were available for each region, and therefore, some variability within the dataset may exist due to potential differences in timing and environmental conditions. No evidence of bleaching or disease was observed in any nursery or outplant location during this study.

Donor colonies

Donor colonies were scouted on reefs with known presence of *A. cervicornis* and were selected based on healthy coloration, size (>25 cm maximum diameter), and tissue cover (90–100% live tissue cover prior to collections). Collections typically included 3–4 branches [mean fragment total linear extension, TLE (SD): MIA = 5.4 (1.9); MK = 10.3 (4.5); LK = 4.5 (2.1); DRTO = 3.3 (0.9); PR = 4.4 (1.4)] or ≤10% of the total colony (Electronic Supplementary Material, ESM, Fig. S1a). Donor colonies were monitored in five regions (BC, MIA, MK, LK, DRTO) for at least 1 yr after fragment collection to determine if fragmentation affected colony survival (all regions) and growth (MIA). The status of donor colonies was determined by estimating percent tissue mortality (0–100%) of each colony. When mortality was observed, the cause of mortality was noted if easily identified (i.e., predation, algal/sponge competition, breakage, disease). All donor colony data were collected during 2009–2010 (except in DRTO where data were collected in 2011).

In MIA, donor colonies, as well as adjacent undamaged control colonies for comparison, were monitored at each collection site. Growth of donor ($n = 20$) and control colonies ($n = 20$) was calculated by measuring linear extension of branch tips marked 2 cm from the apical or fragmented tip with a small cable tie (Shinn 1966; Lirman et al. 2010). Growth was documented for three fragmented and three control (unfragmented) branches within each donor colony, was well as within undamaged control colonies (3 branch tips).

Survivorship of nursery and outplanted fragments/colonies

Fragment/colony survival was determined by counting the number of fragments (within nurseries) and colonies (outplanted onto wild reefs) with some live tissue (if partial mortality was <100%, the colony was considered alive). When mortality was observed, the cause of mortality was noted.

Growth and productivity of nursery and outplanted fragments/colonies

Growth and productivity were calculated for nursery and outplanted corals. Total linear extension (Johnson et al. 2011) was determined for each coral individual using a flexible ruler; measurements of all branches were calculated to the closest cm. Annual growth was determined as change in TLE over time for each coral. Annual productivity was calculated as the amount of coral produced relative to the tissue/skeleton present at the start of the study (annual productivity = growth/initial TLE) as described by Lirman et al. (2014a). Mean annual growth and productivity were calculated by pooling all nursery corals (including all genotypes) or outplants (including all genotypes and sites) for each region. Only fragments with positive growth that were alive for the 12-month period and that did not undergo partial tissue mortality or fragmentation were included within the data set. Thus, our approach documents maximum growth potential by excluding fragments that experienced breakage or partial mortality from the analyses as described by Edmunds (2007). If a total 12 months was not available for TLE measurements, TLE values were extrapolated linearly to calculate 12-month values and, therefore, may underestimate growth due to exponential growth associated with branch development and colony complexity (Lirman et al. 2014a). If corals within a program were not measured using TLE but were assigned into size classes, the median length of each size class was used to calculate growth (i.e., if a colony was binned into a size class of 10–20, 15 cm was used as the TLE measurement). This method was used at MK to collect outplant growth data.

Restoration benchmarks

Restoration benchmarks are usually established in comparison to reference or pristine conditions (Lirman and Miller 2003). However, in the case of Caribbean coral reefs, such conditions no longer exist due to decades of decline in *A. cervicornis* populations. In most cases, corals are grown in nurseries that do not replicate reef conditions and corals are often outplanted onto reefs devoid of surviving *Acropora*. This creates a situation in which restoration metrics such as survivorship and growth can only be compared and evaluated within and among programs, and not against historical or undisturbed conditions. The approach used here is to present regional and overall means from six large-scale programs that have used similar restoration methods (but highlighting methodological differences when appropriate) to measure survival and growth of staghorn donor colonies, nursery fragments, and outplanted nursery-reared corals. Based on these data, we propose simple benchmarks for each step of the coral gardening process that can be used by practitioners to compare their local metrics to those obtained from our extensive database. Admittedly, regional means collapse environmental and genetic/genotypic variability; however, we argue that the value of the proposed simple benchmarks is that they represent a large number of corals from many genotypes that were grown in different environments. Thus, while new programs will not replicate the environmental conditions or the genotypes used in the analyses, they will still be able to compare their success metrics to those proposed, and determine the relative performance of their components. Large departures from the regional means can be used as early warning signals and more exhaustive attention can be paid to those steps of the gardening method that may need to be modified. Similar approaches based on collating large datasets and/or expert opinion have been used extensively to develop benchmarks for water quality (www.reefplan.qld.gov.au), seagrass health (Madden et al. 2009), partial coral mortality (Lirman et al. 2014b), and overall reef health (Kramer et al. 2015). Here, we propose a stop-light framework based on the relative performance (mean) of each region for each restoration criterion, where values within 10% of the overall mean are considered "green" (above proposed desirable benchmark: no action or improvements required), values 10–20% below the mean are considered "yellow" (caution: some adjustments should be made), and values >20% below the mean are considered "red" (action must be taken to improve methods, design, or site selection). These benchmarks are only proposed for sites and years when there have been no large-scale disturbances like temperature anomalies or hurricanes.

Results

Effects of fragment collection on donor colonies

Donor colonies (sample sizes: BC = 20; MIA = 20; MK = 10; LK = 7; DRTO = 20 colonies) were monitored for at least 12 months after fragment collection and all metrics collected indicated limited or no significant

impacts of fragment collection. Tissue mortality was not observed at the lesion site of fragment collection on any donor colonies in any region (ESM Fig. S1b). Only a few donor colonies (one colony at MIA and three colonies at DRTO; 5.1% of all donor colonies) experienced complete mortality. Mean percent tissue cover of surviving donor colonies for all regions combined was high (85.0 ± 5.8%; Fig. 1) 1 yr after fragment collection, with limited partial mortality. Partial mortality was attributed to algal overgrowth, predation (*Hermodice*, *Coralliophila*, and damselfish), or breakage. The MIA donor colonies experienced the highest partial tissue mortality but, importantly, there were no significant differences in mean partial mortality between donor (29.8 ± 8.6%) and control (22.5 ± 7.4%) colonies ($p = 0.278$), further indicating the lack of impacts of collection. In MIA (the only region where both donor and control colonies were monitored), there were no significant differences in growth or productivity between fragmented (mean growth = 6.9 ± 0.4 cm yr^{-1}) or control (mean growth = 6.2 ± 0.7 cm yr^{-1}) branches on the donor colony ($p = 0.337$ and 0.477, respectively) or between branches on the donor colonies and the control (6.7 ± 0.8) colonies ($p = 0.207$ and 0.114, respectively).

Survival of nursery corals

After installation within in situ coral nurseries, mean fragment survivorship over 12 months for all regions combined was high (90.8 ± 4.5%, range 84.8–96.0%; sample sizes BC = 86; MIA = 123; MK = 174; DRTO = 191; PR = 675 corals and 75 total distinct genotypes; Fig. 2). The common sources of tissue mortality within nurseries were breakage (4.2%) and predation (2.9%), while algal/sponge/hydroid competition (2.1%) also occurred but was lower due to nursery maintenance practices.

Growth and productivity of nursery corals

Corals propagated on cement blocks grew between 10.5 (5.9) and 29.5 (20.2) cm yr^{-1} and annual productivity values ranged between 2.6 (1.6) and 6.7 (3.5) among regions during the first year (Fig. 3). The mean growth rate was 17.8 (7.8) cm yr^{-1}, while mean productivity was 4.3 (0.8) ($n = 1456$ corals and 85 genotypes for all regions combined). Significantly higher growth rates (52.5 ± 28.8 cm yr^{-1}) and productivity values (12.3 ± 6.7) were seen for fragments propagated on FUCAs in Puerto Rico ($n = 675$) compared with fragments grown on blocks attached to the bottom (sample sizes: BC = 86; MIA = 123; MK = 174; LK = 207; DRTO = 191; $p < 0.001$). Here, benchmarks were set based on productivity by corals propagated on blocks because all Florida nurseries were initially populated using fixed-to-bottom platforms. Productivity was selected as the benchmark metric to remove the potential confounding effect of initial fragment size on growth (i.e., mean initial fragment sizes ranged from 2.8 ± 0.1 to 10.3 ± 0.6 cm among regions; ESM Table S1; Lirman et al. 2014a).

Survival of outplanted corals

Outplant survival was 85.2 ± 9.7% 12 months after transplantation (range 74.7–93.1%; sample sizes:

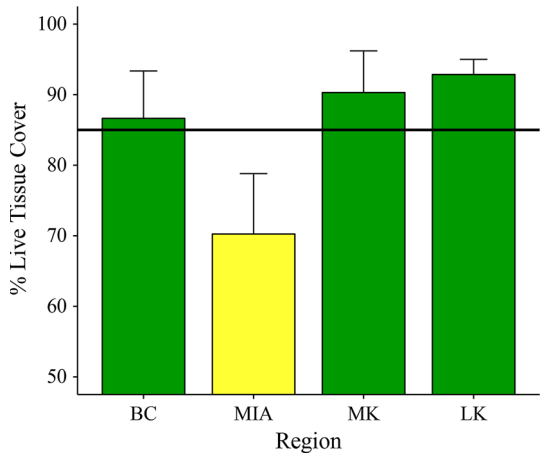

Fig. 1 Percent tissue cover (± SD) of donor colonies of *Acropora cervicornis* 12 months after fragment collection in Broward County (BC), Miami-Dade County (MIA), Middle Keys (MK), and Lower Keys (LK). Bars were colored *green* if values were within 10% of the overall mean, *yellow* if 10–20% below the mean, and *red* if >20% below the mean. Overall mean indicated by *black line*

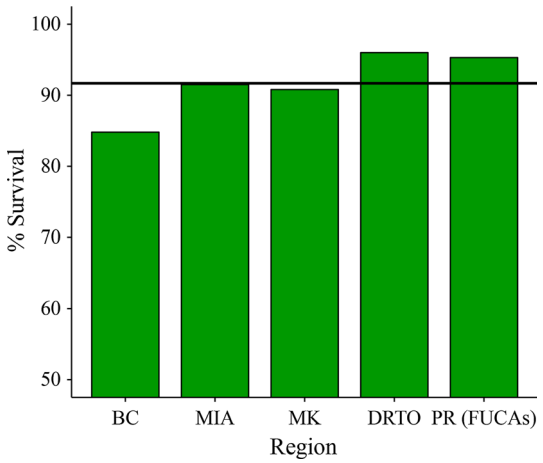

Fig. 2 Percent fragment survival of *Acropora cervicornis* within coral nurseries (all nursery corals combined for each region; Broward County (BC) = 86; Miami-Dade County (MIA) = 123; Middle Keys (MK) = 174; Dry Tortugas National Park (DRTO) = 191; Puerto Rico (PR) = 675 corals). Corals were propagated on cement blocks (Florida nurseries only) and floating underwater coral arrays (FUCAs; Puerto Rico only). Bars were colored *green* if values were within 10% of the overall mean, *yellow* if 10–20% below the mean, and *red* if >20% below the mean. Overall mean indicated by *black line*

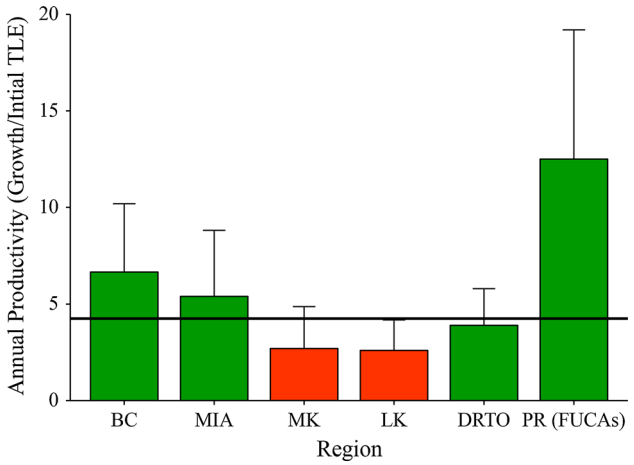

Fig. 3 Mean annual productivity values (± SD) of *Acropora cervicornis* grown on cement block (Broward County (BC) = 86; Miami-Dade County (MIA) = 123; Middle Keys (MK) = 174; Lower Keys (LK) = 207; Dry Tortugas National Park (DRTO) = 191) and floating (Puerto Rico (PR) only; $n = 675$) (FUCA) platforms within in-water nurseries. Annual productivity was calculated as the amount of coral produced relative to the tissue/skeleton present at the start of the study [annual productivity = growth (cm)/initial TLE (cm)] as described by Lirman et al. (2014a). *Bars* were colored *green* if values were within 10% of the overall mean (calculated for corals grown on block only), *yellow* if 10–20% below the mean, and *red* if >20% below the mean. Overall mean for annual productivity (*black line*) is calculated using data collected from block platforms only

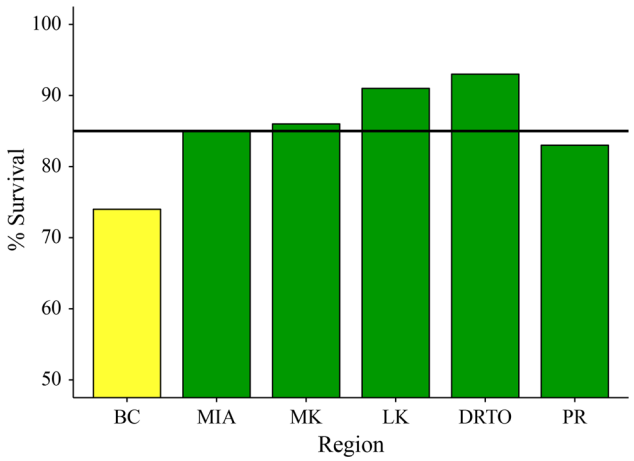

Fig. 4 Percent survival of nursery-reared outplants after 1 yr (Broward County (BC) = 75; Miami-Dade County (MIA) = 264; Middle Keys (MK) = 195; Lower Keys (LK) = 150; Dry Tortugas National Park (DRTO) = 76; Puerto Rico (PR) = 173 corals). *Bars* were colored *green* if values were within 10% of the overall mean, *yellow* if 10–20% below the mean, and *red* if >20% below the mean. Overall mean indicated by *black line*

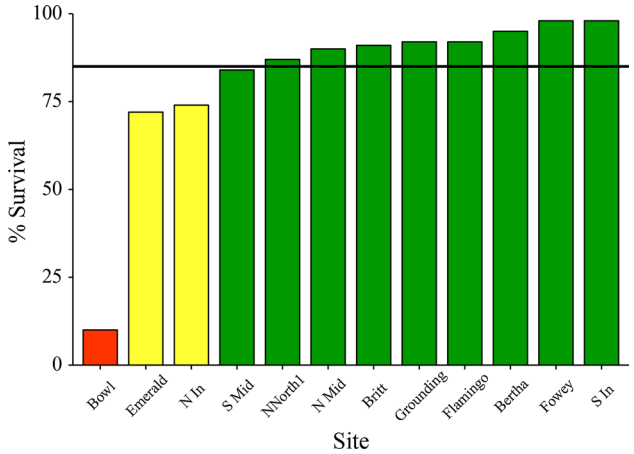

Fig. 5 Survival of outplanted *Acropora cervicornis* at Miami-Dade County (MIA) restoration sites ($n = 150$ corals per site) over 12 months. *Bars* were colored *green* if values were within 10% of the overall mean, *yellow* if 10–20% below the mean, and *red* if >20% below the mean. Overall mean indicated by *black line*

BC = 75; MIA = 264; MK = 195; LK = 150; DRTO = 76; PR = 173 corals; 60 total distinct genotypes, and 25 sites total for all regions combined; Fig. 4). Survivorship of outplants 24 months after transplantation was documented in three regions: BC (4 sites; 66.7%), MIA (6 sites; 79.7%), and MK (4 sites; 78.7%). The most prevalent causes of tissue loss for outplanted corals were breakage (23.6%) and predation (12.5%), similar to causes of mortality of nursery corals. While most regions experienced low levels of mortality, there were important differences in survival of outplants among outplant sites. For example, in MIA, the mean survival of outplants was 82.0 ± 24.1% for 12 outplant sites ($n = 150$ outplants per site) after 1 yr, but one site had significantly higher mortality after outplanting (>90% mortality; $p < 0.001$) due to heavy predation by *Hermodice* and *Coralliophila* (Fig. 5).

Growth and productivity of outplanted corals

Mean growth rates of corals outplanted ranged from 25.6 (13.9) to 80.6 (45.2) cm yr^{-1} among regions, with a mean overall growth rate of 46.2 (20.8) cm yr^{-1} (sample sizes: BC = 75; MIA = 264; MK = 195; LK = 150; DRTO = 76 corals). Mean annual productivity values ranged between 2.6 (0.6) and 11.2 (7.7) among regions, with a mean annual overall productivity value of 4.9 (3.6) (Fig. 6). Initial outplant size ranged from 7.6 (0.3) to 21.3 (9.3) cm among regions and mean annual productivity of *A. cervicornis* outplants was slightly higher than observed in nursery corals (ESM Table S1).

Discussion

In this study, we combined an extensive dataset collected by coral restoration practitioners as part of the US *Acropora* recovery program to document early (1–2 yr) restoration success metrics for *A. cervicornis* during non-stressful

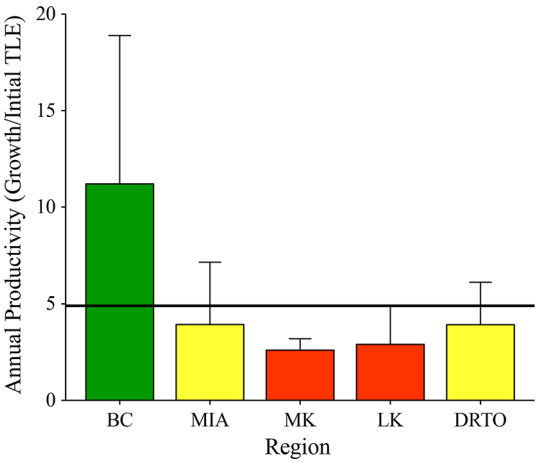

Fig. 6 Mean annual productivity values (±SD) of nursery-reared *Acropora cervicornis* outplants (sample sizes: Broward County (BC) = 75; Miami-Dade County (MIA) = 264; Middle Keys (MK) = 195; Lower Keys (LK) = 150; Dry Tortugas National Park (DRTO) = 76; Puerto Rico (PR) = 173). Bars were colored *green* if values were within 10% of the overall mean, *yellow* if 10–20% below the mean, and *red* if >20% below the mean. Overall mean indicated by *black line*

conditions in Florida and Puerto Rico. By reporting region-specific data on the impacts of fragment collection on donor colonies, survivorship and growth of nursery corals, and survivorship and growth of outplanted corals, we provide the basis for a stop-light indicator framework for new or existing restoration programs to evaluate the performance of the different steps of the coral gardening methodology and to make adjustments when needed. This is the first attempt to collect such baseline data at regional scales and will pave the way for the development of more detailed indicators and benchmarks that can be used to fully assess the progress and impacts of our regional coral and reef restoration efforts in the future.

Donor colonies

Causing damage above natural levels to severely depleted wild *A. cervicornis* populations for nursery propagation would represent an undesirable impact of any coral restoration program, especially those working with threatened or endangered species. Here, we show that the collection of fragments did not negatively impact donor staghorn colonies when <10% of a healthy colony is collected as: (1) no tissue mortality was recorded at lesion sites; (2) >85% live tissue coverage was recorded on donor colonies even after 1 yr; (3) donor and control colonies had similar tissue mortality rates; and (4) there was no significant difference in growth of donor and control branches. The impacts of fragment collection on donor colonies can vary among species and even within *Acropora*. While Epstein et al. (2001) found high mortality in *Stylophora* when >10% of the colony was removed, Lohr et al. (2015) found that small *A. cervicornis* colonies may be fragmented up to 75% with no significant effects. Based on our observations, we suggest the removal of <10% of coral tissue from large, healthy donor colonies as a conservative guideline for initial staghorn collections. When these guidelines are followed and fragments are collected from corals with ~100% live tissue cover, a benchmark of 76% live tissue cover (survival) 1 yr after collection is proposed. Based on this benchmark, the MIA donor colonies appear to have suffered some impacts from fragment collections (~30% mortality, classified as "yellow"). This is the type of result that would indicate that collection methods or colony selection procedures may need to be modified. However, in this case, there were no significant differences in tissue mortality between donor and control (unfragmented) colonies, indicating that all colonies in the Miami region naturally experience tissue losses that are higher on average than those observed within other regions in our study. With this knowledge, benchmarks for MIA (or elsewhere where these patterns are evident) can be adjusted as experimental data are collected. Lastly, further controlled studies such as those conducted here for *A. cervicornis* need to be performed for other species as new taxa are added to propagation programs in the Caribbean.

Nursery survival

The very high survivorship of fragments observed at all nurseries combined (only 9.8% of fragments showed 100% mortality) demonstrates that the methods used for the collection, transportation, and deployment of *A. cervicornis* fragments within nurseries are very efficient and do not cause excessive mortality. This is a consistent result across programs and it is not unreasonable to propose a benchmark of 80% survivorship of staghorn fragments within nurseries over the first year after collection. Large deviations from these survivorship values may reflect a genotype or genotypes that are particularly ill-suited to nursery conditions, a sub-optimal nursery environment, or inadequate collection, transportation, and deployment methods. In extreme cases (e.g., several cohorts classified as yellow or red), nurseries may need to be re-designed or moved to a more appropriate location (guidelines for the selection of nursery sites and recommended nursery maintenance appear in Johnson et al. 2011).

Nursery productivity

Coral growth is a true integrator of environmental conditions and, when measured within common gardens (i.e., nursery, single reef sites), provides a metric that can be easily used to assess site and genotype performance (Lirman et al. 2014a). Growth rates measured within the

staghorn nurseries were equal to or higher than growth rates reported for wild *A. cervicornis* (Shinn 1966; Gladfelter et al. 1978; Tunnicliffe 1983), reinforcing the earlier finding that in-water nurseries, even those established in non-reef habitats (e.g., on sandy channels, over seagrass beds), provide an excellent growth environment for propagated staghorn corals (Lirman et al. 2010). In addition, nursery methods have changed over time to promote significantly higher growth rates even between propagation platforms, as seen when comparing nursery growth of staghorn corals on fixed-to-bottom blocks verses mid-water floating FUCAs. Here we report both growth (change in colony size) and productivity (growth normalized to initial colony size) to explore the potential use of these metrics as simple benchmarks. Lirman et al. (2014a) showed that growth of staghorn coral is linearly related to colony size and number of branches. Thus, when growth is compared among fragments or colonies from different cohorts or programs, it is important to note the average size of the units used to avoid using inadequate null hypotheses. Using productivity as a performance metric for *A. cervicornis* resolves the issue of the relationship between size and growth. The mean regional productivity values of staghorn corals grown on blocks attached to the bottom (Johnson et al. 2011) ranged from 2.6 to 6.7, with an overall average of 4.4 (>1500 corals from 85 genotypes). The mean productivity value of outplanted corals ranged 2.7–11.2, with an overall mean value of 4.8. A nursery productivity benchmark value of 4 and an outplant productivity value of 4.3 can be used to rank the performance of staghorn genotypes within a program and compare performance across nurseries (that use fixed-to-bottom propagation platforms) and reef sites. Growth and productivity of staghorn corals appear to be much faster when grown on suspended platforms such as FUCAs, lines, or PVC trees (Nedimyer et al. 2011; O'Donnell et al. 2017). In fact, most *Acropora* restoration programs now either maintain a combination of both types of platforms or have switched completely to floating platforms. As shown for the high productivity of staghorn corals grown in FUCAs in PR (productivity value = 12.3), productivity benchmarks would need to be adjusted based on growth platform as more data on growth of suspended corals are collected.

Unlike the survivorship benchmarks proposed for nurseries that may be used to modify the collection or nursery steps of the gardening program, the productivity benchmark should only be used for the identification or ranking of fast- and slow-growing genotypes within a program. However, productivity values can still be used to inform nursery operations. Slow-growing genotypes may need to be fragmented more frequently to maintain maximum growth rates (Lirman et al. 2014a), while fast-growing genotypes may need to be outplanted sooner to prevent a given genotype swamping nursery capacity. The goals of nursery operations are to minimize coral mortality and maximize productivity. However, the goals of outplanting go beyond these two nursery goals to include the establishment of genotypically diverse restored populations (Lirman and Schopmeyer 2016). This last goal will require the propagation of coral genotypes with both high and low productivity within nurseries. Also, because performance within a nursery is often not predictive of performance when outplanted, and genotypes may have widely different growth rates in different environments (Lirman et al. 2014a; Drury et al. 2017), we suggest that practitioners do not disregard genotypes that consistently rank below the proposed benchmark from their program. Slower-growing genotypes may be more resistant to disturbances such as temperature anomalies and, thus, should also be maintained within nursery broodstock. Finally, unlike survivorship, a metric that can be collected quickly, measuring growth and productivity of staghorn corals is a time-consuming process and is commonly only performed on a subset of corals of each new genotype brought into the nursery or outplanted onto the wild. While researchers have proposed using coarser and less time-consuming colony measurements such as diameter and height to estimate colony growth (Kiel et al. 2012; Huntington and Miller 2013), we presently lack benchmarks for these approaches within our database.

The regional productivity data provide a frame of reference for new programs but also help highlight large-scale patterns of habitat suitability that need to be further investigated. One example of the value of these data is the documentation of very high mean productivity of both nursery (6.7) and outplanted (11.2) staghorn corals in Broward County, Florida. Broward County is home to the best developed staghorn thickets in Florida (Vargas-Ángel et al. 2003; Walker et al. 2012) and the documentation of the highest regional productivity values here suggests favorable environmental conditions (and possible refugia) for this threatened coral species in this area. Such productivity gradients can be used to develop testable hypotheses to explore growth and environment relationships in support of future restoration and management decisions.

Outplant survival

A crucial step in the coral gardening process is the outplanting of corals back onto natural reefs where, if successful, they will increase reef complexity, build valuable habitat, and sexually reproduce to increase genetic diversity and aid in the recovery of *A. cervicornis* (Lirman and Schopmeyer 2016). Mean survival of outplants across regions during years where no major disturbances were documented was 85.2%, representing higher survival than

experimental outplanting conducted in previous *A. cervicornis* studies (Becker and Mueller 2001; Fogarty 2012). Thus, we propose a benchmark of 77% for the survivorship of outplanted corals during the first year. In this study, deviations from this value were attributed to predation, damselfish occupation (Schopmeyer and Lirman 2015), disease, and physical removal and breakage. While some of the attributes of a good outplant site can be assessed prior to outplanting (e.g., depth, coral cover, presence of living wild staghorn, no disease), the presence of small, cryptic predators like *Coralliophila* and *Hermodice* is harder to assess visually and may only be detected based on impacts recorded after outplanting, as seen in our Bowl site in MIA where 90% of corals were lost to predation (Fig. 5) (see Johnson et al. 2011 for a description of site-selection guidelines). Therefore, the use of small-scale pilot plots to evaluate site and genotype performance prior to full outplanting is suggested to improve overall outplant survival and success (Johnson et al. 2011).

Within the field of coral reef restoration, research is presently focused on identifying site-specific biological and physical variables that may explain and predict outplanting success (Wirt et al. 2013). Wirt et al. (2015) developed an interactive tool to help inform *A. cervicornis* outplanting and restoration site prioritization based on current environmental and ecological data such as species richness, coral cover, connectivity, species interactions, and reef health. As more data on the influence of habitat (and genotype) become available, benchmarks of outplanting success will need to be adjusted accordingly (Drury et al. 2017). Nevertheless, even when expert judgment was used (as it has been the case in the last 10 yr in the USA), the mean survivorship of >80% of outplanted staghorn corals after 1 yr (a figure that integrates a wide range of genotypes and environments) is a remarkable achievement of the *Acropora* recovery efforts. The three programs that measured survivorship beyond the first year showed that mean outplant survivorship after 2 yr dropped to 75% (only an additional 10% mortality). As more programs collect survivorship data over longer intervals, benchmarks beyond the first year can be developed using the proposed framework.

One of the more important outcomes of our project is that, based on survivorship and growth, nursery-grown *A. cervicornis* colonies behave similarly to wild colonies once outplanted (ESM Fig. S1c, d). Further evidence of this is the growing number of observations of the synchronous spawning of both wild and nursery-reared staghorn corals. Nursery-reared outplants are reaching sexually reproductive sizes within 2 yr of outplanting and developed gonads have been found in nursery corals in Florida (BC, MIA, MK, and LK) 2–3 yr post collection (Authors pers. obs.). Outplants have been observed spawning within at least two regions of the Florida Reef Tract (BC, MK) showing clearly that outplants created through coral gardening can contribute to sexual reproduction in this species. Similar findings have been reported for the congeneric *A. palmata*, where colonies reared from larvae spawned only 4 yr after being outplanted onto natural reefs (Chamberland et al. 2016).

The main goal of this study was to use our extensive regional data to propose simple propagation and outplanting benchmarks for practitioners and managers with useful metrics to evaluate the performance of the steps of the coral gardening framework for recovery of depleted *Acropora* populations in the Caribbean. A key component for the sustained success of ecological reef restoration is to develop standards to hold practitioners accountable for the responsible propagation and outplanting of corals (Lirman and Schopmeyer 2016). Based on analyses of a consistent, large regional dataset, we show that the coral gardening methods used to propagate and restore *A. cervicornis* populations are very effective, that no excess damage is caused to donor colonies, and that once outplanted, staghorn corals behave just as wild colonies. We also provide science-based benchmarks that can be used to evaluate successes and challenges of coral gardening efforts and to make modifications where needed. Here, we propose that up to 10% of the biomass can be collected from healthy, large donor colonies for nursery propagation. We also propose the following benchmarks for *A. cervicornis* during the first year of activities: (1) >75% live tissue cover on donor colonies; (2) >80% survivorship of nursery corals; and (3) >70% survivorship of outplanted corals. Finally, we report productivity means of 4.4 for nursery corals propagated on fixed-to-bottom platforms and 4.8 for outplanted corals as a frame of reference for the ranking of genotype performance within programs.

While the data described here are all from the US, other regions within the Caribbean may use these suggestions or develop benchmarks for their specific programs using similar approaches. If a project fails to meet accepted benchmarks, adaptive strategies should be used to improve performance. For example, high mortality within a nursery may indicate that the nursery should be relocated to an area with better water quality or a more sheltered location to avoid storm damage. High mortality at an outplant site may indicate poor water quality, that predator removal is necessary, or that attachment methods should be adjusted. Finally, in addition to the benchmarks proposed here, expanded benchmarks should be developed for other crucial steps in the restoration process such as the contribution of outplanted corals to reef structure and coral cover, the number of corals developing and releasing gametes, and the diversity and structure of the fish and invertebrate community supported by restored sites. Such benchmarks,

and subsequent adaptive actions, are needed to fully assess the long-term success of coral restoration and species recovery programs.

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