Session 42A

Propagation and active reef restoration – techniques and considerations for the production of corals and propagules and transplantation onto degraded reefs

Session chairs:

Tom Moore, tom.moore@noaa.gov

Sarah Frias-Torres, sfriastorres@gmail.com

David Vaughan, dvaughan@mote.org

Phanor Montoya-Maya, phanor@natureseychelles.org

Diego Lirman, dlirman@rsmas.miami.edu

Claude Reveret, claudereve@yahoo.fr

Edwin A. Hernandez-Delgado, coral_giac@yahoo.com

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The efficacy of nursery head-starting in the culture and restoration of *Acropora cervicornis*

Andrew M. Ross

Abstract The growth and vegetative propagation of coral in nursery culture provides an option for active and targeted redevelopment of degraded reef function. However, the specific hardening and head-starting elements of nursery culture are not fully illustrated. In this study, four lineages or presumed distinct genetic lines of *Acropora cervicornis* from 12m depth were collected, grown and monitored bimonthly for 12 months through 2006 and 2007 in mid-water horizontal line nurseries at 3, 7 and 15m depths in Montego Bay, Jamaica. These corals were then re-fragmented and propagules randomly re-set to new nurseries in the same locations wherein they were similarly monitored for a further 10 months to assess the potential of nursery head-starting in propagative coral culture. The second, propagative iteration's corals started at faster per-apical polyp growth rates than the previous wild-sourced for the first 100 days ($p<0.001$), suggesting head-starting. Differences between parent coral lineages in growth ($p<0.001$) and branching rates ($p<0.001$) of the first nursery iteration persisted into the second regardless of initial or secondary nursery depth, as did the relative resistances to temperature stress of those lineages ($p<0.001$). This coined the relative descriptive terms "strong" and "weak" for these lineages; a concept relevant to culture at restoration scales in a warming sea. A trend towards hardening to bleaching was also noted in the second iteration corals. Per-polyp extension rates reached and plateaued at a similar apparent maximum rate in each nursery iteration that coincided with the initiation of branching. This suggests partitioning of limiting resources between energy-consuming activities and metabolic resources, photosynthetic surface area and available light.

Keywords: *Acropora cervicornis*, coral culture, coral nursery, coral restoration, head-starting

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Andrew M. Ross
Seascape Caribbean, Montego Bay, Jamaica

Communicating author: Andrew M. Ross, ross.andrew@mac.com

Introduction

Coral nurseries provide a relatively protective environment, controlling for inhibitors such as predation, abrasion, competition and sedimentation to enhance survivorship and growth (Soong and Chen 2003; Rinkevich 2006; Shafir et al. 2006). These protected conditions allow coral nurseries to use tiny fragments of a few or even a single or partial polyp called nubbins (Shafir et al. 2006) and microfragments (Forsman et al. 2015), generating much working propagative capital with very little initial wild-harvest investment. As such, a nursery programme may use small amounts of wild-harvested coral material to produce a much larger crop for re-fragmentation to further expand production, out-planting back to the wild for enhancement and restoration, or for scientific experimentation, all without need to return to the wild stocks. This multi-step process is modelled on terrestrial silviculture (Epstein et al. 2003) and is here coined "anthozoculture" to reflect this, particularly at restoration scales. It is a useful option to recover depleted corals that play key ecosystem roles, such as is the case of the genus *Acropora* in the Western Atlantic (ABRT 2005).

Several authors have shown that damage or stress may decrease a corals ability to reproduce, particularly after storms (Lirman 2000) or bleaching (Mendes and Woodley 2002), suggesting that metabolic resources are limited. Acroporids transport such resources from areas of production in the photosynthetic radial polyps to areas of rapid use at the apical polyps (Gladfelter 1985; Fang et al. 1989) and corals under better conditions, thus with more resources, should also be able to grow and expand more quickly (Gladfelter and Monahan 1977; Shafir et al. 2006). Nurseries have similarly shown improvements in coral fecundity over their wild counterparts (Horozsowski-Fridman et al. 2011) further suggesting improved resource availability or stores in the nursery. As such, reducing stresses to a growing coral should improve fecundity as well as growth.

Ecological restoration more generally suggests replacement of species and services of an ecosystem such that it may regain its pre-disturbance condition and function (SER 2004). Such restoration often employs captive head-starting to allow juveniles of key species to attain a size refugia to their predators or competitors, or to build enough resource reserves to improve survivorship through to reproduction. Silviculture grows large numbers of tree seedlings to sizes best suited for a given planting condition, including both ecological and logistical factors and anthozoculture would strive to do the same (Epstein et al. 2003). In damaged, harvested or restored corals, improved survivorship has been shown in larger fragments, through escape from full predation in both natural and human-facilitated regeneration processes (Knowlton et al. 1990;

Bowden-Kerby 1997). In the nursery, larger fragments have similarly seen higher survivorship by outgrowing their spatial competitors by increasing the ratio of undamaged to stressed material when stressing organisms are confined to the nursery surface (Soong and Chen 2003).

This study looks at elements of stress, healing and growth and the transfer of nursery-derived improvements thereto into daughter vegetative fragments, employing successive iterations of controlled and protected in situ nursery culture under anthozocultural models. Its outcomes will inform programmatic design as scales increase towards relevance to ecosystem restoration.

Methods

This work follows two successive nursery iterations, or harvest and then propagative fragmentations, through their respective growth seasons. In the following, these will be described by the shorthand Frag1 and Frag2.

In March 2006, 6 Buoyant Drop-Loop Line (BDL) or "String" nurseries were set along the intercontinental fibre-optic cable to the west of the Sangster International Airport, with 2 at 3m in the back-reef adjacent to the outer-most landing light, 2 at 7m in well-developed buttress reef and 2 at 15m in a large sand-patch adjacent to the reef wall (Fig. 1). These nurseries were set with upper and lower horizontal nursery lines at 60cm and 100cm from the substrate, with each line pre-set with 10 drop-loops approximately 20cm apart. These nurseries were populated with 5cm unbranched fragments of *Acropora cervicornis* on 19th and 21st March collected from four lineages (presumed-distinct genets) from around the Montego Bay area at 12m depth. Coral fragments were colour-coded for individual tracking with a fine nylon-coated wire. This wire was then used to securely tie the propagule to the nurseries drop-loops in a random pre-set pattern, with each nursery holding five fragments of each lineage. The sample was tied at the approximate middle, with care taken to retain its original up-down orientation. The random set pattern was repeated through the three depth-locations (N=120). Though the distance between the harvested parents strongly suggested that these parent corals were not related, this was not tested directly. Therefore, the term lineage is used rather that the more usual term genet.

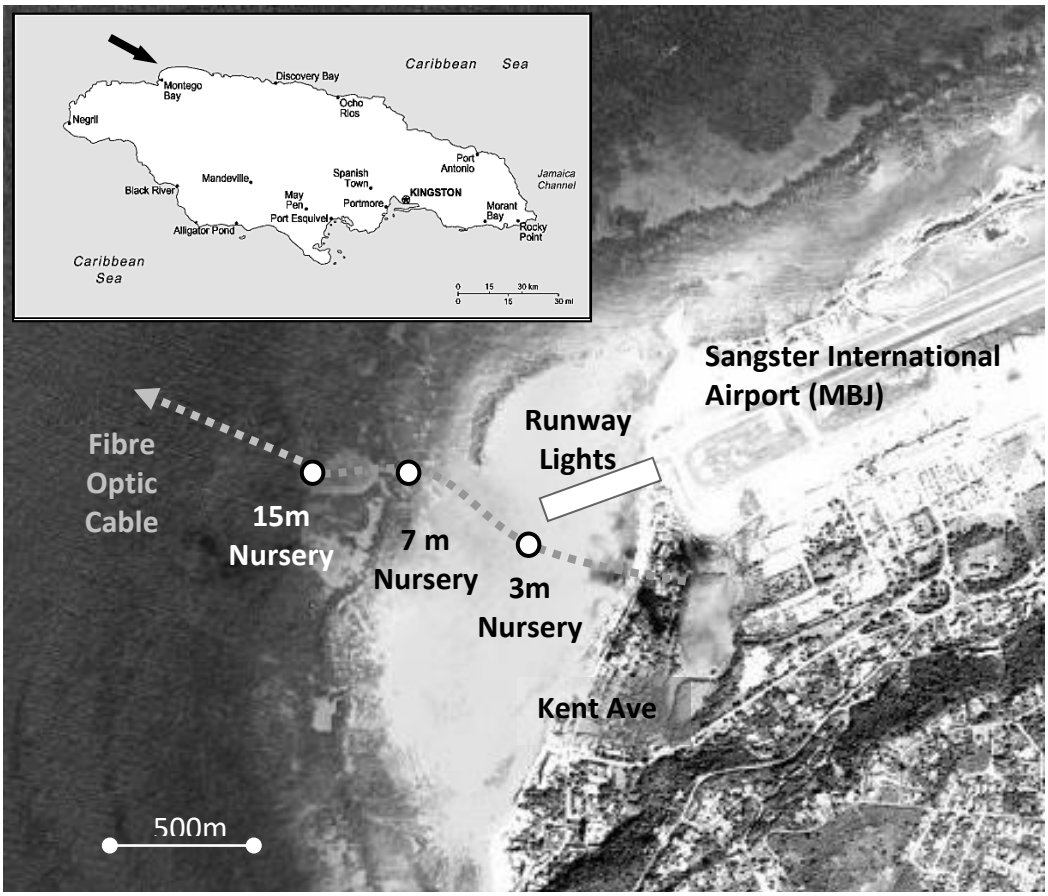

Fig. 1 Coral nursery locations at 15m, 7m and 3m depths in the northeastern portion of the Montego Bay. The 3m nurseries are in a low relief back-reef pavement adjacent to the final of the airport runway lights. The 7m site is in a wide sand-channel of the area's well-developed buttress structure shoreward of the Airport Reef scuba diving site, and the 15m site in a sand patch within 20m of the continental shelf at the Widowmaker's Cave scuba site

These corals were maintained and monitored at 9, 16 and 48 days initially, then approximately bi-monthly through a total 12 month period. Monitoring visits included coral measurement and a per-coral assessment of stress affects such as colour or tissue loss and any observable source of stress.

Coral measurements were taken along the primary branch length (extension) from apical tip to apical tip along its longest axis. Total coral length (expansion) added this to the combined measurement of each branch from apical tip to its origin, as per Bowden-Kerby (1997). A branch count was also made from emergence of each apical bud.

One sample was lost and not replaced in a line-fishing tangling incident at the 15m deep fore-reef site prior to the first measurement on day 9. Another fishing-tangling incident prior to day 308 removed a further 7 samples from the other nursery at 15m. Further mortality resulted from bleaching in the 3m back-reef nurseries.

Bleaching was noted in all samples at 3m during the 10th September (day 172) visit and all samples of lineages Orange and Green were dead by the following visit of the 15th November (day 240). Surviving samples had recovered colour by the November visit.

Bleaching stress was also noted in the 7m nurseries, with partial bleaching and paling in the Blue and White lineages and complete bleaching in the Orange and Green. All had recovered by the November visit. Green and Orange 3m are under-represented by 33% in the Frag2 iteration and this is accounted for in the analysis, including analyses only to or for visit 5, the 15th November. Changes in N values are in Table 1.

In May 2007, these nurseries were moved to adjacent concrete blocks to make way for new nurseries similar to the previous, though with 12 drop-loop attachment points at each level over the two independent nurseries.

A random template was generated assigning locations for each lineage and also for each depth-location of the previous year, with four samples taken from each location for each lineage for the three repeat-nursery locations. Drop-loop spaces for Orange or Green colour-coded lineages from the Frag1 3m nurseries were left empty. Therefore, 40 samples were set per location, made up of 12 each of lineages marked with Blue and White and 8 each of Orange and Green (N=120).

Unbranched 5cm coral fragments were harvested from the original nurseries and set to the new nurseries per the methods described for the Frag1 iteration on 4th June. These Frag2 nursery samples were measured and monitored approximately every second month for 10 months with methods as per the previous year with the same measuring diver.

To account for inaccuracies in cutting 5cm coral propagules underwater, the metric extension is used rather than the actual fragment length. Extension is the fragment length along the main axis less the sample's initial length at day 28. Similarly, expansion is the additive length of all branches minus the initial day 28 length, alternatively referred to as Total Linear Extension or TLE.

Fishing line entanglement removed one sample in the 15m nursery between deployment and first measurement of the Frag2 iteration that was not replaced. Furthermore, one of the two nurseries of the Frag2 generation at the 15m was damaged by an errant Antillean Z fish-trap between visits 1

and 2, leaving all samples either abraded or dead. The data of that nursery was discarded. The 3m shallow back-reef nurseries were relocated to 11m depth on 18th August for Hurricane Dean, which impacted Montego Bay on 19th August. The nurseries were returned to their back-reef location on 26 August. Paling and partial bleaching occurred in the 3m nurseries in the 19th October visit (day 109) and all had recovered by the following visit on 20th December (day 199).

The months of iteration commencement are uneven, with measurement 2 of the Frag1 occurring in May and for Frag2 in August. These visits and changes in N values are in Table 1.

Results

Coral growth comparisons between nursery iterations

The corals of the Frag2 iteration were healed and growing at a faster rate than the Frag1 by the second Frag2 measurement visit at day 74 (Fig. 2a). Frag2 was not surpassed in extension rate until day 105, suffering likely seasonal temperature stress. Both iterations reached a maximum extension rate of 0.62mm/day (SD ±0.30) which was not significantly different for day 172 in Frag1 and 199 in Frag2 ($p= 0.906$, Fig. 2b). This maximum rate represented a plateau in the Frag2 iteration (Fig. 2b-c), which was not encumbered by particular bleaching event at that season. In both iterations this maximum extension rate, including plateauing thereof, coincides with the time of secondary branches emergence; approximately day 180 and 130mm of extension in the primary axis, or 180mm total sample length (Fig. 3, 4)

The likely temperature related Frag2 decrease in extension rate into the third measurement was not significant (One-Way ANOVA $p= 0.919$). Between days 199 and 352 the Frag2 iteration also has a reduction in extension rate (Fig. 2c) observed to be related to nursery overgrowth and inter-sample contact damage that also did not prove significant ($p= 0.967$).

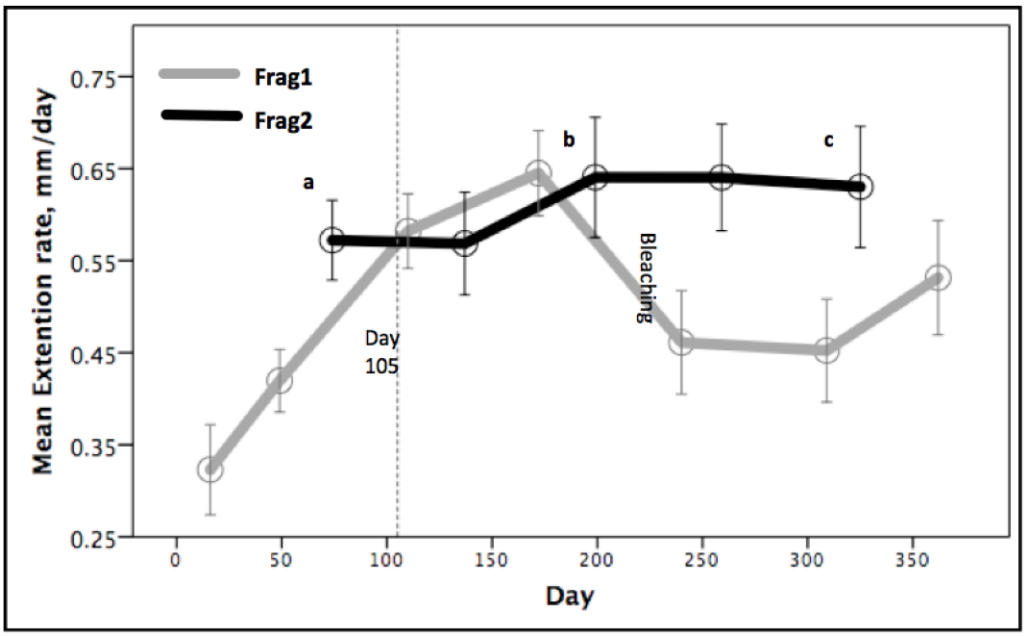

Fig. 2 Mean daily extension rates over time for the Frag1 and Frag2 nursery iterations expressed in millimeters per day per day. (±the 95% Confidence Interval) N-values in Table 1

Frag1 accelerated in extension rate until day 172, when growth rate slowed corresponding with a seasonal temperature and bleaching event. Differences between the Frag1 and Frag2 daily extension rates are significant in the time-pooled data, with the Frag2 iteration corals growing at a faster rate (One-Way ANOVA $p < 0.001$). The pooled mean extension rate of $0.54 mm \cdot d^{-1}$ (SD ±0.29) equates to $8.8 cm \cdot yr^{-1}$ per apical polyp.

In Frag1 up to and including day 308, 4 corals had extension rates of beyond $1 mm \cdot d^{-1}$, or an averaged approximately $18 cm \cdot yr^{-1}$ per apical polyp and at day 362 six corals had extension rates over $1 mm \cdot d^{-1}$. In the Frag2, the extension rate was equal to or more than $1 mm \cdot d^{-1}$ on 23 occasions: 2 at day 74, 3 in day 137, 9 in visit 4, 4 in visit 5 and 5 in visit 6. The mean Frag2 rate of $0.61 mm \cdot d^{-1}$ (SD ±0.30) equates to $11 cm \cdot yr^{-1}$ per apical polyp, though this is likely skewed relative to Frag1 by underrepresentation of the bleaching-susceptible lineages. The fastest observed daily rate for any sample was 1.41 $mm \cdot d^{-1}$, which equates to $26 cm \cdot yr^{-1}$ per apical polyp.

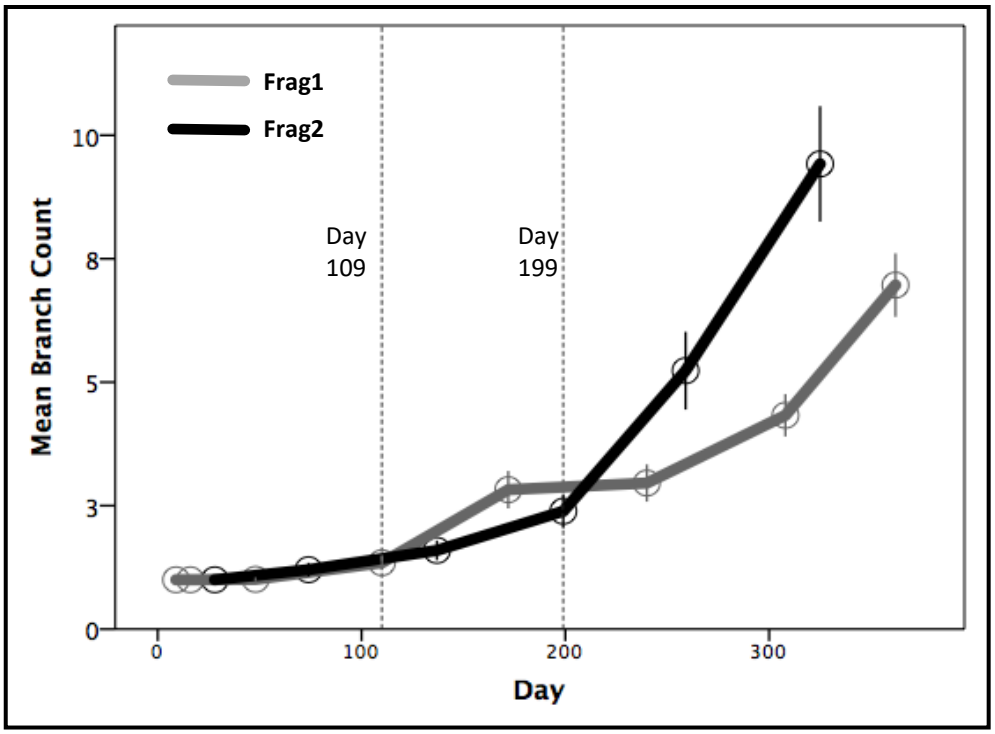

Fig. 3 Mean per coral branch count over time for the Frag1 and Frag2 nursery iterations. (±the 95% Confidence Interval) N-values are in Table 1

The Frag1 set first branches between days 110 and 172, prior to the bleaching event registered at day 172 and before particular branching occurred in the Frag2 (Fig. 3). During the bleaching recovery period no new branches were produced in Frag1, while over this same period the Frag2 had its initial branch formation. Branching after day 109 in the Frag1 and 199 in the Frag2 corresponds with the points of maximum extension rate in Figure 2. Particular branching in Frag2 from day 199 corresponds with the end of rate acceleration and plateau of b-c in Figure 2.

In coral expansion, the Frag1 generation expands significantly less than the Frag2 (One-Way ANOVA $p < 0.001$) with the primary break between the two corresponding with the Frag1 bleaching event at day 172 and particular branching in Frag2 from day 199. The characteristic exponential-type expansion curve may be seen in the unencumbered Frag2 iteration (Fig. 4).

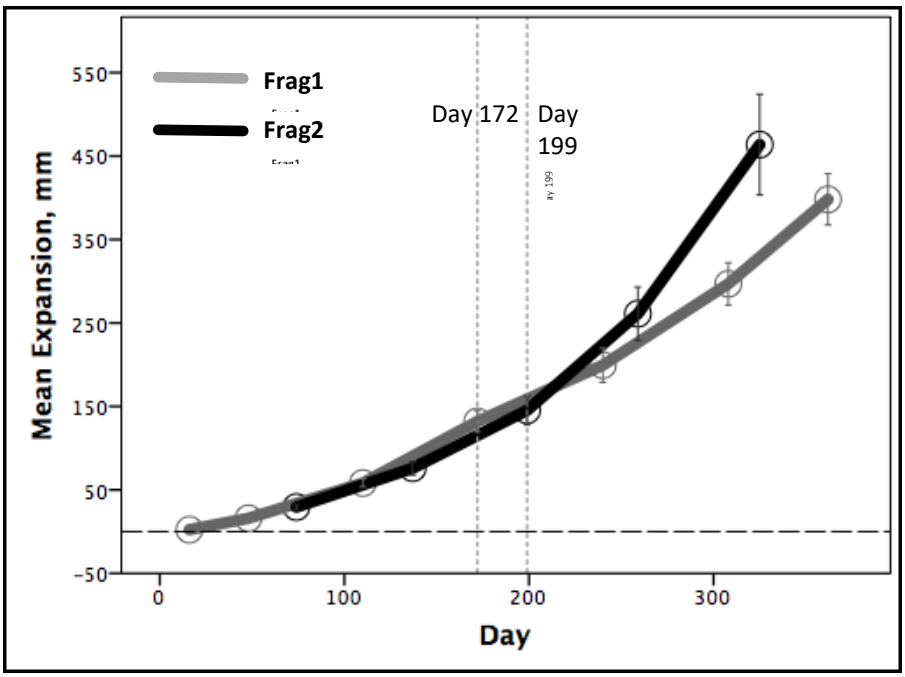

Fig. 4 Mean per coral expansion over time for the Frag1 and Frag2 nursery iterations. (± the 95% Confidence Interval) N-values are in Table 1

Bleaching and growth

In non-parametric testing, the observed level of bleaching is negatively correlated with extension rate (Spearman's rho r <0.001), branch count (Spearman's rho r= 0.029) and with expansion rate (Spearman's rho r <0.001). The graphs for extension rate of Figures 2, 3 and 4 illustrate this relationship as the periods of reduced relative production occur at similar times to bleaching in each iteration.

Lineages and depths

In General Linear Model (GLM) ANOVA testing of the Natural Log of the daily expansion rate pooled for the full experimental period controlling for factors location (depth) and lineage along with nursery iteration (Adjusted R Squared= 0.347) shows significant differences between the nursery locations (p <0.001) with 7m shallow fore-reef being the strongest and the 3m shallow back-reef being the poorest performer in both Tukey and Gabriel post hoc testing. There were also significant differences between the lineages (p <0.001) with the White and Blue forming a stronger

homogenous subset and the Green and Orange forming a second subset in both Tukey and Gabriel post hoc testing. The significance of iteration ($p < 0.001$) suggests that iteration also independently affected expansion rates (Fig. 5), though it is not controlled for bleaching per se beyond proxies in lineage, location and nursery generation and the following interactions thereof.

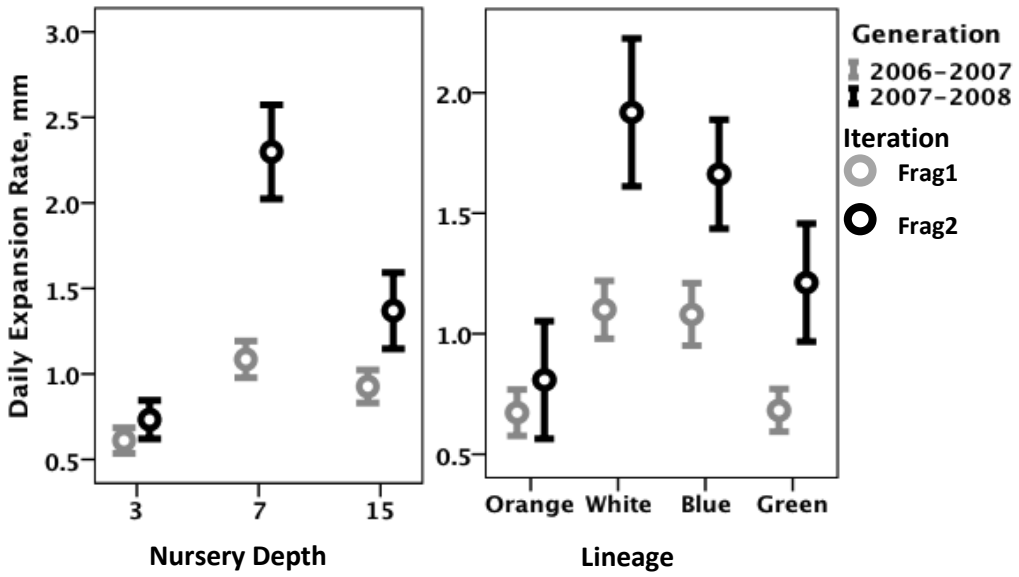

Fig. 5 Expansion rates per iteration, per nursery depth and per lineage. (±the 95% Confidence Interval). N-values are in Table 1

The aforementioned GLM (ANOVA) analysis shows significant interactions between lineage and depth-location ($p < 0.001$), lineage and generation ($p = 0.006$) and location and generation ($p < 0.001$) affecting the expansion rate, likely related to bleaching. All lineages performed better in the Frag2 iteration but for Orange in Figure 5, which only trended to a stronger Frag2 generation.

Bleaching adaptation in Frag2

Bleaching was not prevalent in the Frag2 iteration; however, some samples did show upper-surface paling or bleaching on day 137, 19th October. These samples were in the back-reef nursery and of the Orange or Green lineages only. Even without a full bleaching event, a trend towards adaptation may be seen in Figure 6, whereby the corals that were susceptible to bleaching in the Frag1 and survived, namely the Green and Orange in nurseries of the shallow fore-reef at 7m, show a trend towards reduced susceptibility in the Frag2 when compared to the corals of the deep fore-reef

nurseries in the Frag1 that showed little or no bleaching. This adaptive trend is more apparent in the more affected Green lineage in Figure 6.

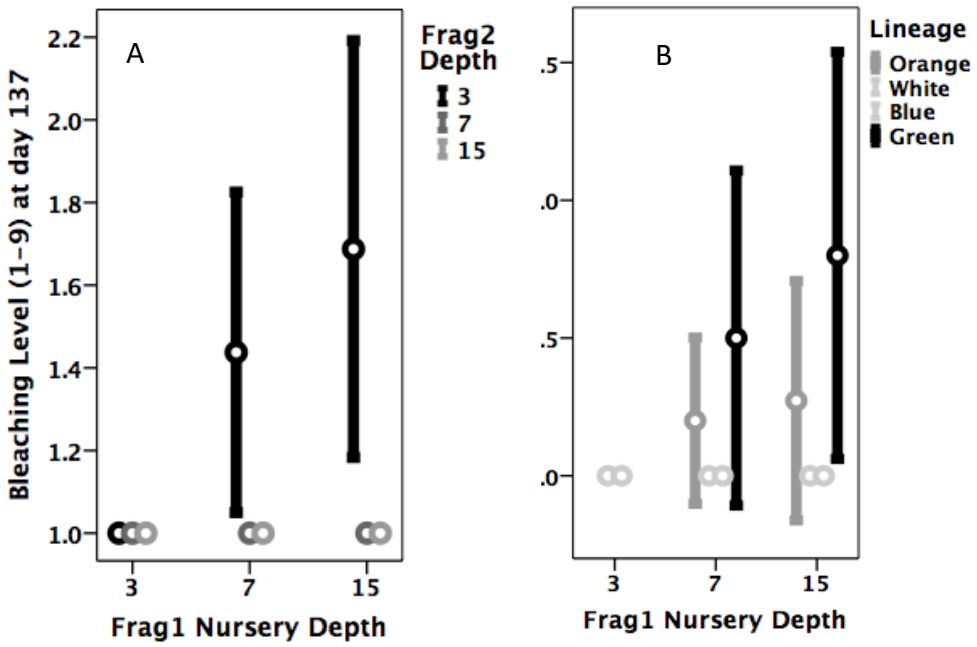

Fig. 6 Bleaching levels for (A) the Frag1 nursery depths at day 137 only per Frag2 depth and (B) per lineage in the 3m back-reef site of the Frag2 iteration only. (±the 95% Confidence Interval). N-values are in Table 1

Table 1. Dates of sample set and measurement of the two nursery iterations. The rows are set to approximately align the visits

Frag1, 2006-2007					Frag2, 2007-2008			
Date	Days in Nursery	Visit	N		Date	Days in Nursery	Visit	N
19,21 March: wild corals set to nurseries					June 4th: nursery corals reset			
29/03	9		119		June 13,14: monitored, unmeasured			
5/04	16	1	119		2/07	28	1	119
5,9/05	48	2	119		17/08	74	2	100
7,9/07	109	3	119		19/10	137	3	100
6,10/09	172	4	119		20/12	199	4	100
15/11	240	5	119		18/02	259	5	100
18,26/01	308	6	91		24/04	352	6	100
17/03	362	7	91					

Discussion

This experiment used in situ nursery culture to isolate and explore resource and growth patterns in *Acropora cervicornis* under the broader theme of coral and ecosystem restoration, following repeated iterations of like lineage material through like conditions in elevated line nurseries. This research found that nursery propagated fragments of *A. cervicornis* performed better than did their wild-harvested predecessors, healing and growing more rapidly through the first 100 days. This suggests improved metabolic resources available through time spent in the nursery; a process known in horticulture as head-starting. Though sought and illustrated specifically here, such head-starting was largely expected, as accelerated growth in the nursery as compared to wild and literature derived values has been illustrated by several authors in this and other species (Bowden-Kerby 2001, Shafir et al. 2006; Lirman et al. 2014). Improved fecundity and other elements of general vigour have also been illustrated in nursery corals (Horozsowsi-Fridman et al. 2011). Programmatically, this suggests that wild harvested fragments of *A. cervicornis* be held in the nursery for a period prior to out-planting as a matter of course, in particular fragments of opportunity that may be stressed at collection. Alternatively, head-start is likely to be relative to the sample's starting vigour, thus particularly healthy wild corals may see little such improvement with nursery time.

The second iteration, nursery-sourced corals showed a faster mean extension rate until day 105, when the first iteration surpassed it due to elevated seasonal temperature stress in that second iteration year. Absent such an event, the improved extension rates of that second iteration may have persisted until other elements of nursery life or resource partitioning provided slowing influence. Both nursery iterations found a maximum mean extension rate of $0.62mm.d^{-1}$(SD ±0.30) or approximately $11.6cm.yr^{-1}$ per apical polyp, with the first iteration showing this rate at day 172 prior to bleaching and the second once it had recovered from seasonal temperature stress at day 199. Once the second iteration reached this rate, it retained this rate through the remainder of the experimental season. As such, this apparent maximum per-polyp extension rate represented a plateauing of the previously accelerating extension rate, suggesting either a maximum rate for the lineages and conditions, as suggested by Bowden-Kerby (2001), or another such restriction. The fastest extension rate achieved by any coral of this experiment was $1.4mm.day^{-1}$ which equates to $24cm.year^{-1}$ per apical polyp, though one of the two extending polyps that make up the extension value was likely faster again.

In both iterations of this experiment, this maximum or plateaued extension rate corresponded with the initiation of particular branching, suggesting trade-offs related to limiting metabolic and growth-related resources, per Gladfelter (1985) and Fang (1989). This maximum polyp extension rate and branching point occurred circa 130mm of new growth and 180mm of total coral length, which speaks to timelines for greatest programmatic efficiency to refragmentation or out-planting. It also coincides with the reproductive puberty length of 17cm described by Soong and Lang (1992) for this species, though spawning was unlikely to have impacted resource allocation through the timelines of the second iteration.

Parent coral lineages

Coral parent lineage or genet has been shown here and previously as a primary driver to growth rates (Lirman et al. 2014), thus direct comparison between the same lineages, including as tested-distinct genets, is necessary in assessing method or site performance. This work found that better and lesser growth rate lineages persisted regardless of nursery location, depth or nursery time. This study followed the same lineages through sequential iterations, illustrating the benefits of nursery time regardless of propagule heritage. Furthermore, the faster growing lineages were the least susceptible to temperature events and bleaching in all nurseries and conditions. Works seeking to establish bleaching resistant populations through propagative culture (Bowden-Kerby and Carne 2012) with limited nursery space and resources may begin by establishing relative extension rates of potential parent corals, and preferentially populating their nurseries with the fastest growing available lineages that are also likely to be the most temperature tolerant.

In the first, wild-sourced nursery iteration, two lineages were seen to grow faster in all locations and conditions. These lineages were also the least susceptible to fouling and to bleaching stresses and therefore were dubbed “strong”, with the others being the “weak” lineages. These patterns of relative strength and weakness persisted through the second, propagative nursery iteration. As the first iteration were all harvested from 12m depth and produced similar lineage differences to the second iteration derived from nurseries at multiple depths and conditions, we may surmise that these differences are controlled at the lineage or clonal level rather than according to the growth environment. Though these differences suggest genetic heritage, they may also be due to zooxanthellae, chronic disease or other aspects taken from the parent that could not be bolstered in nursery head-starting. They may also result from clonal age: a vigorous youth and elderly

senescence. Such senescence has been shown in the elder portions of standing *Acropora* colonies (Meesters and Bak 1995) but it has not been shown on a patch colony or clonal scale. The over-reef expanse of the parent colonies that might provide a relative age, per Hughes (1984), was not measured in this experiment. However, clonal ages as described Devlin-Durante et al. (2016) suggest ages far beyond what this hypothesis might allow for.

Nursery function

The illustrated growth improvements may be derived from several independent, additive or synergistic aspects of nursery life. An elevating nursery's corals are held up and away from a rugose substrate and fully exposed to the benefits of water flow (Patterson et al. 1991; Gardella and Edmunds 1999) and light (Gladfelter 1985) both direct and reflected from turbidity and high-albedo substrates. Sediment has been shown to reduce growth rates in coral (Crabbe and Carlin 2007) and a nursery holding samples above the substrate while exposing them to moving water to mitigate any accumulation will be of benefit. Sediment also may harbour disease (Patterson et al. 2002), while disease may also be vectored by predators including the polychaete *Hermodice caruncula* (Sussman et al. 2003). Such cryptic corallivores appear to be unwilling suffer exposure such as larger expanses of sand (Quinn et al 2005), which appears to extend to crossing mid-water lines, though they may recruit directly from the water column (Shafir et al. 2006). *Stegastes planifrons* did not colonize nursery corals in either iteration, though this damselfish was observed to be abundant on the adjacent reefs.

On the reef, macroalgae compete for space with the corals and shade and abrade the corals directly (Lirman 2001; River and Edwards 2001) and may also harbour disease (Nugues et al. 2004). Algae may entangle or recruit to the nursery; however, the BDL nursery employed in this research was developed to minimize the amount of structure in proximity to the coral samples, therein reducing fouling loci (Soong and Chen 2003). Macroalgae were not particularly problematic even with the bimonthly visits of this experiment. The primary fouling organisms were colonial hydroids including *Halochordyle disticta* that did cause occasional, patchy stress where colonization proved chronic.

An anthozocultural approach to coral restoration through multiple nursery iterations prior to out-planting, per Epstein et al. (2003), would include head-starting incidentally. In this, to assume no bleaching in the Frag2 of Figure 2 and cautiously extrapolate its early accelerating extension rate

line based on the later Frag2 and Frag1 accelerations, the second iteration may have reached the aforementioned maximum extension rate and initiated branching as early as day 100, with corals less than 130mm total length. This is a vital consideration as propagative culture thinks towards general conceptual industrialization for ecosystem restoration scales. To focus on high-growth lineages for production as well as temperature stress resilience, a progamme may reach to this point even sooner. As this experimental result suggests trade-offs in apical polyp extension and formation related to limiting metabolic resources, approaches that force branching through fragment orientation (Soong and Chen 2003) or targeted abrasion or cuts should be approached with caution.

Bleaching

The first, wild-harvest nursery iteration paled or bleached briefly soon after nursery setting, particularly in the shallower locations, returning colour by the following visit at day 16. This is attributable to the stress of harvest and new (light) conditions. However, bleaching was notable in the shallower sites through the warmer months of August through November, with mortality of the weaker lineages at 3m, but full recovery of colour in all remaining samples by November. A particular drop in extension, expansion and branching rates occurred during this period, with recovering acceleration not noted until March. Harvest and relocation stress paling the second nursery iteration was light and only at the 15m to 3m relocated samples and had recovered by day 28; however, a period of paling at the 3m site in the weak lineages was noted in October. The mean extension rate stops increasing during this period and branching appears to be delayed relative to the previous iteration. Generally, this experiment found bleaching, including relatively mild seasonal temperature events that may not involve zooxanthellae loss, to stress the samples and inhibit growth. Arguably, the resetting of the second iteration was ill-timed, though this may have been worse-so had it been the first, wild-sourced iteration.

Bleaching resilience

This work suggests corals that bleached and recovered in the first iteration showed a distinct trend towards reduced bleaching when bleaching was expressed in the second iteration. Bleaching was generally mild in the second iteration and only expressed in the weak lineages and only as mild and upper-surface paling, thus significance was not achieved in this observed adaptation or hardening

trend. This was exacerbated as many of the weak corals that bleached in the first iteration also succumbed to that bleaching, thus were not represented in the second.

The second generation nurseries were populated with corals of the previous nurseries with random redistribution of samples between the depths, including those of depths that did and did not suffer bleaching in the first iteration. In the mild bleaching event of the second year, corals from the deeper fore-reef systems that showed little paling in the first iteration tended to show more paling in the second as compared to those from the shallow fore-reef site that bleached properly and recovered in the previous year. This suggests that corals have the capacity to adapt to non-lethal bleaching conditions over a relatively short period of time, in this case a single exposure. This does not necessarily suggest that bleaching is adaptive per se (Buddemeier and Fautin 1993; Baker et al. 2004), but it does suggest that hardening of an independent isolate may occur through innate or zooxanthellae-related mechanisms.

The general relative resistance of the stronger lineages remains the driving force in overall bleaching susceptibility as these corals remained the least susceptible even after hardening of the weaker lineages. However, a useful tool in propagative restoration may be controlled sub-lethal bleaching to force adaptation to increasing temperatures, particularly in such weaker lineages to keep them in the overall population and contributing to total reproductive potential and genetic diversity long-term. Initial harvests focusing on areas of known greater regular temperatures will also be useful, per Edmunds (1994). During the bleaching event of in the first nursery iteration the surrounding wild reef showed no particular loss of colour in any species. The nursery corals harvested from 12m depth were not so adapted.

The particular exposure of the nursery corals to light and water may have also contributed to their susceptibility to seasonal stresses such as temperature and possibly also UV light. This would be corroborated in that paling was noted in the 12m fore-reef nurseries in the first generation but not in the wild reef of the same depth, and that bleaching was not seen on the wild reef at any depth during the second iteration year. As such, a high-exposure nursery such as the BDL may provide a useful tool not only in propagation, but also in the forced adaptation to local bleaching related stress of corals for restoration.

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