The effects of interspecific interactions on the growth of *Acropora pulchra* and *Porites cylindrica*

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Corals in the Order Scleractinia are popular marine ornamental invertebrates within the aquarium trade. Although there are over 100 commercial facilities worldwide that grow and sell coral fragments, 99% of the coral fragments introduced into the aquarium trade still originate directly from tropical reefs. Propagating captive corals is considered a way to reduce the harvesting pressures on natural reefs. However, land-based facilities are limited by space and costs associated with growing large quantities of coral. To address the financial constraints of the facility and meet the demand for corals in the aquarium trade, commercial coral farmers must maximize coral growth and quantity within the confines of space-limited, land-based facilities. This study investigated the growth responses of two coral species cultured together. The close proximity of *Porites cylindrica* resulted in an increase in growth (length, weight, and branch development) for *Acropora pulchra*. Conversely, *P. cylindrica* exhibited a reduction in growth (length, weight, and branch development) in treatments where *A. pulchra* was in close proximity. These results show that, contrary to the current practice of spacing corals at distances that prohibit any type of interaction, *A. pulchra* will show an increase in growth due to the presence of *P. cylindrica*. The faster growth rates will lead to a higher production of corals and may ultimately aid in further reducing the number of corals harvested from wild stock for the aquarium trade.

Introduction

Corals in the Order Scleractinia are popular marine ornamental invertebrates within the aquarium trade (Carlson 1996, Delbeek and Sprung 1997). In 2005, the Convention on the International Trade of Endangered Species (CITES) reported that over 1.5 million pieces of live coral were traded globally. Green and Shirley (1999) estimated the retail value of the live coral trade at US$50 million per year. Although there are over 100 commercial facilities worldwide

that grow and sell coral fragments, 99% of the coral fragments introduced into the aquarium trade still originate directly from tropical reefs (Wabnitz et al. 2003). Propagating captive corals is considered a way to reduce the harvesting pressures on natural reefs. Recent advances in captive coral propagation, as well as the demand for corals, has led to an increase in the number of commercial land-based facilities dedicated to culturing corals (Sykes 1997, Rinkevich and Shafir 2000, Delbeek 2001). However, land-based facilities are limited by space and costs associated with growing large quantities and species of coral. To address the financial constraints of the facility and meet the demand for corals in the aquarium trade, commercial coral farmers must maximize coral growth and quantity within the confines of space-limited, land-based facilities. A concern for commercial coral farmers when addressing these challenges are: interactions among corals due to space limitations in the culture tanks.

Competition among corals has been investigated both in the field and in aquaria for decades (Lang and Chornesky 1990). While there have been many investigations into the role of competition on the spatial distributions of corals in the natural environment (Bradbury and Young 1983; Cornell and Karlson 2000), aquaculture facilities have not investigated the importance of spacing distances in culture tanks (Rinkevich and Shafir 2000). As our understanding of the complexity of competitive interactions and their consequences on the growth and health of corals increases, a more thorough understanding of the effects of competition could result in strategies that maximize the use of limited space and promote the co-culturing of different species.

Corals are mixotrophic, sessile organisms that require space to access environmental resources such as sunlight and food. Water circulation brings food and aids in gas and nutrient exchange between the coral and seawater (Sebens et al. 1998; Finelli et al. 2006). Reef organisms dependent on sunlight, including most corals, are often restricted to the upper reef slope and reefflat zones. As a result, available space is often limited due to intense competition (Connell 1973). Therefore, the ability of corals to grow and survive can often be attributed to how well they compete for space on the reef (Lang and Chornesky 1990).

Corals compete for space using a variety of mechanisms (Lang and Chornesky 1990). These mechanisms can be divided into two broad categories: Direct and Indirect (Connell 1973). Direct mechanisms involve physical confrontation with encroaching competitors. The result of these confrontations is the loss of tissue from one or both of the competitors. Indirect mechanisms do not involve physical contact and include overtopping and allelopathy. Many corals use both direct and indirect mechanisms, while other corals specialize in one type (Lang and Chornesky 1990).

Among the many types of direct mechanisms, extracoelenteric digestion, the use of sweeper tentacles, and overgrowth are the strategies most often observed. *Extracoelenteric digestion* makes use of mesenterial filaments, extruded from the gut and used to digest the soft tissue of the subordinate. Lang and Chornesky (1990) found that this is the most common mechanism for corals engaged in physical confrontations. Further, Lang (1973) found that many of the consistently dominant corals employed this type of mechanism. *Sweeper tentacles* are specialized for defense and are up to ten times longer and contain larger, more potent

nematocysts than ordinary tentacles (Hidaka and Yamazato 1984). Many corals that mainly rely on sweeper tentacles tend to have either slow growing, massive or encrusting, low profile growth forms (Lang and Chornesky 1990). In the absence of physical disturbances, corals with these morphologies may become overtopped by fast growing, branching corals or become subordinates to corals with more powerful extracoelenteric digestive capabilities. Wellington (1980) and Richardson et al. (1979) found that corals with sweeper tentacles effectively maintained space by preventing more dominant corals from growing within the range of the sweeper tentacles. *Overgrowth,* the ability for a dominant coral to use the subordinate skeleton as substrate for expanding its growth, is a mechanism that involves a more permanent form of dominance over a subordinate coral (Potts 1976). Physical reach limitations of sweeper tentacles or extracoelenteric digestion often restrict aggressive corals from causing damage to the entire subordinate colony. This allows other parts of the subordinate colony to continue to grow (Romano 1990). Further, if the aggression ceases to continue then the subordinate colony may be able to regenerate new tissue in the damaged areas. Dominant corals using overgrowth can ultimately grow over the entire colony or prevent the ability for the subordinate corals to regenerate new tissue (Lang 1973).

Direct competition requires high energetic investments from the coral (Romano 1990). Often, resources are allocated away from growth and reproduction in favor of developing and maintaining mechanisms for competition. This can have negative consequences for both corals engaged in physical confrontations. Rinkevich and Loya (1985) found a significant reduction in calcification rates and the number of female gonads per polyp in both competing colonies of *Stylophora pistillata*. Further, the coordinated cycle of reproduction was altered.

Tanner (1997) examined the effects of competition on growth rates and reproduction of *Acropora hyacinthus* and *Pocillopora damicornis*. Both species exhibited a 50% reduction in growth rate when engaged in direct competition with another species. Reproduction may have also been affected indirectly since fecundity is a function of colony size. Therefore, the reduction in growth could result in a reduction in the total number of gonads within each colony. Ultimately the cost to produce competitive structures must be an investment made by the coral in order to maintain their space within a highly competitive environment.

Indirect mechanisms are used primarily by branching and massive corals such as acroporids and poritids (Baird and Hughes 2000, Connolly and Muko 2003). Overtopping and allelopathy are two types of indirect mechanisms. *Overtopping* occurs when a coral grows above its neighbors and restricts important environmental resources such as sunlight and water circulation to underlying colonies. Rogers (1979) created artificial shading over a portion of the reef and measured the growth rates for *Acropora cervicornis.* In the shaded area *A. cervicornis* colonies grew slower (0.5cm/yr) compared to those in the unshaded area (8 cm/yr). Stimson (1985) conducted a study on the coral abundance beneath the table coral, *Acropora hyacinthus.* Irradiance under the table coral was reduced to 1% of the open reef. *Acropora spp.* and *Pocillopora verrucosa* fragments transplanted from well-illuminated areas of the reef to the shaded area under the table coral showed slower growth and increased mortality. Overtopping also reduces water circulation underneath the coral canopy (Huston 1985). Therefore, corals that may be tolerant of reduced light levels may still not thrive in an environment where water circulation is diminished (Sheppard 1979, Huston 1985). *Allelopathy* has been well documented in many marine organisms (Coll et al. 1982, Sammarco et al.

1983). Although alleleopathy has yet to be clearly demonstrated in scleractinian corals, some authors have found instances where it may be the most likely mechanism operating in the competitive interaction. Bothwell (1983) observed no recruitment in areas surrounding massive corals such as Lobophyllia, Leptoria, Favia, and Goniastrea. However, the zone of "no recruitment" was well beyond the physical reach of the coral's tentacles, suggesting the release of some type of water-borne chemical that prevented larval recruitment near the colony may be operating. Rinkevich and Loya (1983) found that even when colonies of *Stylophora pistillata* were separated by a distance beyond the reach of physical contact, subordinate colonies of would grow away from the dominant colony. These observations in each experiment led each of the authors to conclude that in the absence of any direct contact or overtopping, there was still a mechanism operating that prevented larval recruitment near the massive coral or affected the growth of competing *S. pistillata* colonies. Overtopping also requires energy from the coral, but the energy is invested in growth rather than the development of structures used for physical confrontations. Therefore, growth rates are the important element of such corals in their ability to compete for space on the reef.

Many aquarists and commercial farmers have observed their captive-raised corals using a variety of competitive mechanisms including overgrowth, extracoelenteric digestion, sweeper tentacles, and overtopping (Shimek 2003; Delbeek pers comm.). Because some competitive interactions result in negative effects on competing colonies, most commercial farmers spread corals far apart from each other. Due to the lack of information on proper spacing, farmers often make subjective decisions on how far apart each coral will be spaced. Delbeek (pers.

comm.), for example, suggested that corals should be placed at least at 3 cm apart, though the distance may widen as the corals grow larger.

Spacing corals to avoid competition could mitigate potential negative effects. However, this practice may increase the costs associated with growing the coral to a marketable size. Food, lighting, water movement and water quality control all represent overhead costs in the form of equipment, electricity, and manpower (Wheaton 1993). These costs can be a direct function of space in the tank. For example, the cost to providing adequate lighting to a culture tank is determined by the electrical costs, measured as kilowatts / hour, and the equipment costs, measured in watts / gallon. A general rule for maintaining healthy corals is 3-5 watts / gallon (Tullock 2001). The electrical costs are a function of the amount of wattage used; therefore the cost to provide adequate lighting for a 1000 gallon tank would be significantly higher than the cost for a 100 gallon tank. Profits for a coral-propagating facility are generated by the number of corals it can sell and the speed in which they can be grown to marketable sizes (Ellis and Sharron 1999). The number of corals in a facility is a function of the size of the culture tanks and the number of corals per tank, determined by the spacing. Spacing corals far apart would reduce the total number of corals per tank and require the facility to maintain larger tanks, resulting in increases in overhead costs. Growing corals quickly to marketable sizes would allow the facility to distribute a larger quantity faster. There is a significant difference, therefore, in the facility costs between corals that reach marketable sizes in three months versus six months. These issues can be summed to the question: Can the optimum spacing of corals be a way to maximize the number of corals per tank and promote the fastest growth rates?

One approach to help address this question is to review the knowledge gained by the experience of commercial agriculturists growing ornamental and consumable plants. Investigations into the life strategies of plants have led to the development of better techniques for agriculture. Plants and corals display comparable characteristics in that both are photosynthesizing, sessile organisms who require environmental resources such as sunlight, to grow. Their dependence on these resources often limits the areas where they can exist and the ability to compete for space is an important element towards their success in growth and survival. Finally, similar to corals, plants exhibit effective direct and indirect competitive mechanisms including overtopping and overgrowth. The similarities between plants and corals may make techniques in agriculture applicable to the culture of corals.

Investigating the role of interaction among plants and the effect of spacing on crop yields has led to the more efficient use of the land and increased plant yields. Huddleston and Young (2004) experimented with the spacing of bluebunch wheatgrass (*Pseudoroegneria spicata*) and Idaho fescue (*Festuca idahoensis*) in relation to established individuals of Lemmon's needlegrass (*Achnatherum lemmonii*). Each species was planted at 6, 12, and 18 cm apart from the needlegrass. Both *P. spicata* and *F. idahoensis*, at the 6 cm distance, exhibited 50% reduction in basal growth when compared to the 12 and 18 cm distances. However, *F. idahoensis* were 23 – 38% taller in the 6 cm distance than in any of the other treatments, including those grown in isolation. These results allowed the authors to determine the minimum distance necessary for the successful co-existence of both species. Shehu et al. (2001) used the desert plant, *Lablab purpureus,* to measure the total yield and nutritive value of the crop when grown in high densities. Plants were grown at 70, 110, and 150 cm distances.

Total yield increased as plant densities increased (yield ha^{-1} was greatest when the plant distance went from 110 cm to 70 cm). In the semi-arid region where the study was conducted, the increased densities may have reduced the effects of drought during the dry season. These studies have allowed agriculturists to use optimum spacing as a tool to increase plant growth rates and yields as well as maximize the space in which they grow.

Applying the approaches used by agriculture to those of coral culture may reveal valuable techniques to optimize tank space and increase growth rates. While direct competition is usually avoided due to the potential for physical damage, indirect competition may prove to be an effective tool. To stimulate early growth, overtopping corals that are grown in crowded multi-species environments maybe induced to grow faster compared to those grown in isolation. Dizon and Yap (2000) suggested that the lower growth rate observed for *P. cylindrica* in monospecific cultures may be due to a lack of competition between the corals. Raymundo (2001) found that fragments of *Porites attenuata* placed next to live conspecific neighbors grew faster in terms of linear extension and total surface area compared to those grown next to dead control neighbors. Many branching and massive corals would be good candidates for such an approach as they also display characteristics that are popular within the aquarium trade.

To determine the optimum spacing distances and the effects of interaction on two species of branching corals cultured together, I will ask the question: Will growth be affected for each of the two species of corals cultured together at three different spacing distances? The outcome

of this experiment can be applied to the development new techniques in the *ex situ* culture of corals.

Hypothesis 1:

Ho: There will be no significant difference in growth among the clones for each of the two species of coral fragments cultured together in three spacing treatments

H_1: There will be a significant difference in growth among the clones for each of the two species of coral fragments cultured together in three spacing treatments

To test this hypothesis, measurements were made on growth rate (linear and basal width) throughout the study period; total growth (Weight), the number of new branches and, branch orientation for each coral fragment at the end of the experiment. Each species was treated separately in the analysis of the data.

Methods

Selection of study species

Three criteria were used to select coral species for this experiment: 1) each species should exhibit a predominantly branching morphology; 2) species should have a history of acclimating easily, in terms of survival and growth, to the cultured environment; and 3) species should be found in an environment with parameters similar to the artificial lab environment designed for this experiment. The water table and container designs are described below and are most similar to reef flats where strong sunlight, moderate water circulation and fluctuations in water temperature are the dominant conditions. Coral colonies selected for this experiment were from the Luminao reef flats. Luminao is located on the seaward side of the Glass Breakwater,

a jetty that defines the North side of Apra Harbor. *Acropora pulchra* and *Porites cylindrica* are both found on Luminao reef flats and conform to all of the criteria listed above.

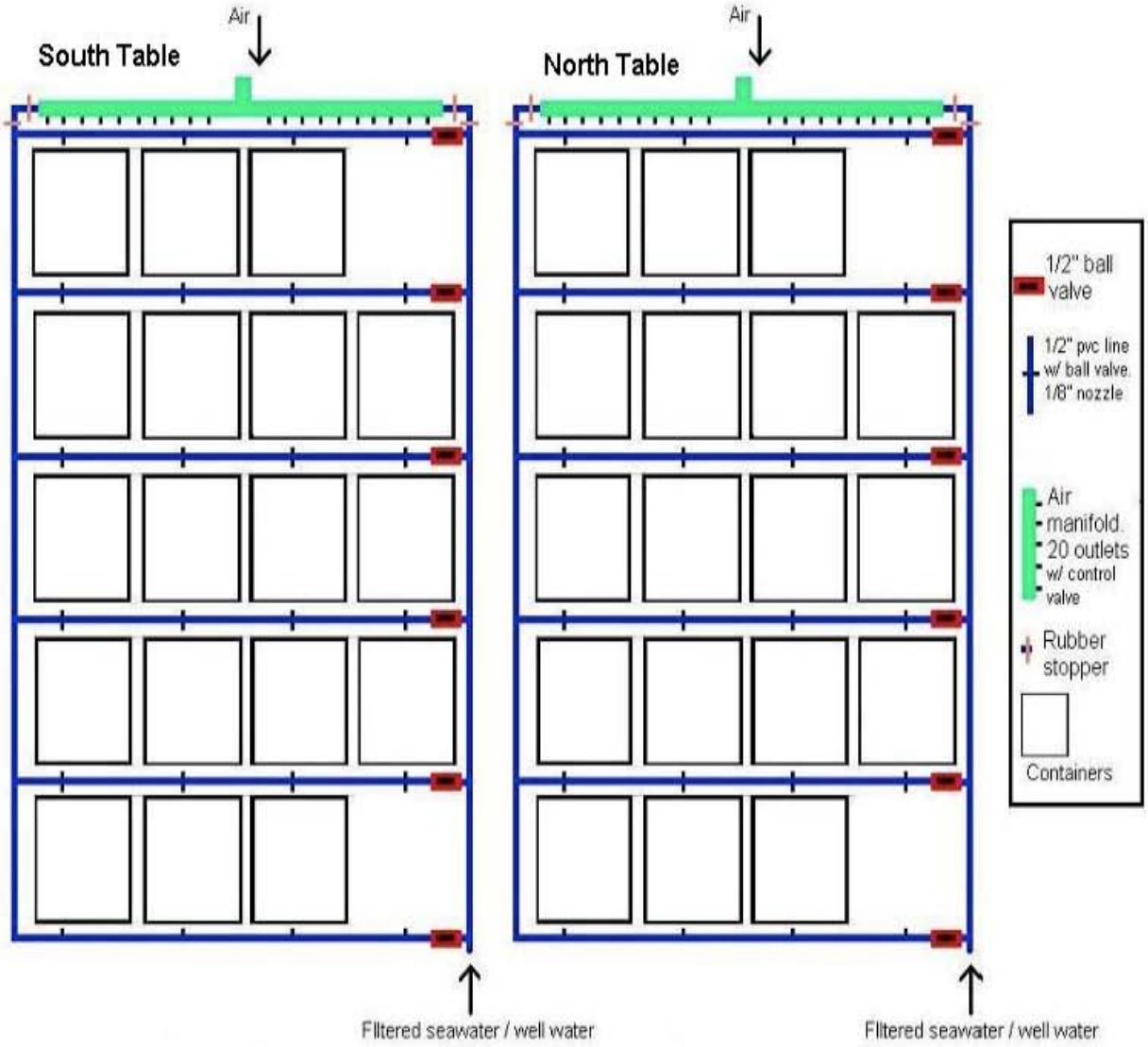
Collection

Twelve *Acropora pulchra* and twelve *Porites cylindrica* donor colonies were located in Luminao reef flats. Donor colonies were at least 10 m apart to minimize the possibility that they were clones (Potts 1976). Bone cutters were used to cut six un-branched fragments measuring at least 45 mm in length from each colony. These were then transported in seawater immediately to the University of Guam Marine Lab. After a two hour acclimation period, the fragments were cropped to a pre-determined length of 35 mm and an epoxy base was added. Clonal groups were spatially separated to avoid mixing genotypes.

Culture set-up

Two covered water tables (North table and South table, Figure 1) were placed side by side in direct sunlight on the East Lanai at the University of Guam Marine Lab. Each water table was fed by a water line that delivers seawater from Pago Bay. A mechanical filter (Pentair Aquatics AF-94, twenty nine inch filters) was used to filter out large particles (>20 microns). Air was supplied to each table from lines coming off the main air compressor at the Marine Lab. One air source and two seawater sources were supplied to each container. Water flow rates between containers were not statistically different (Mean = 12.31 ml s^{-1}, +/- 0.13; ANOVA; $F = 0.36$, $P = 0.5547$ @ $\alpha = 0.05$, Tukey-Kramer North table = South Table).

Figure 1. Water table design. Two tables placed side-by-side on the northern lanai at the University of Guam Marine Lab. Each table held 18 flow-through containers that were serviced by seawater and air manifolds.

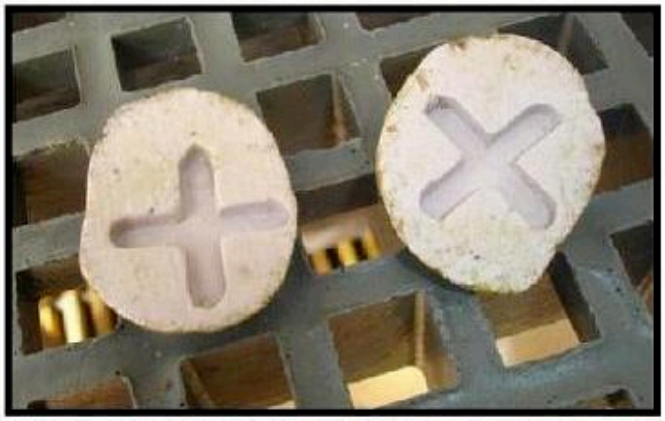


Epoxy base and container design are shown in Figure 2a-c. Each container had a tile spacer glued into the appropriate distance location (Fig 2a). The same tile spacer was used to create an indent in the fragment base. This ensured that the exact position of the fragment was

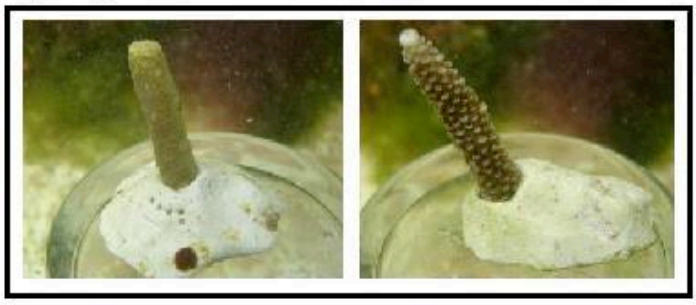
maintained throughout the experiment. Exact orientation for each fragment within the container was obtained by taking photographs of the initial layout of the fragments within the containers.

Figure 2a-c. Container and epoxy base design. Containers were designed for flow-through seawater; epoxy bases were designed to keep the fragment oriented and stable throughout the study period.

a. Tile spacer glued into pre-determined distances



b. The underside of the epoxy base with the tile spacer indent. This allowed the fragments to 'mate' with the tile spacer glued into the treatment containers



c. Top view of the epoxy base with embedded fragment
Left: *Porites cylindrica*. Right: *Acropora pulchra*.

Corals were fed daily with approximately 2.5 g (pre-hatched) *Artemia franciscana* (GSL Premium 90% hatch). Containers and epoxy bases were cleaned twice per week. Mechanical filters were replaced every two days with a set of filters washed in freshwater. Prior to installing the re-conditioned filters, they were soaked in seawater to condition them for use. Rows and

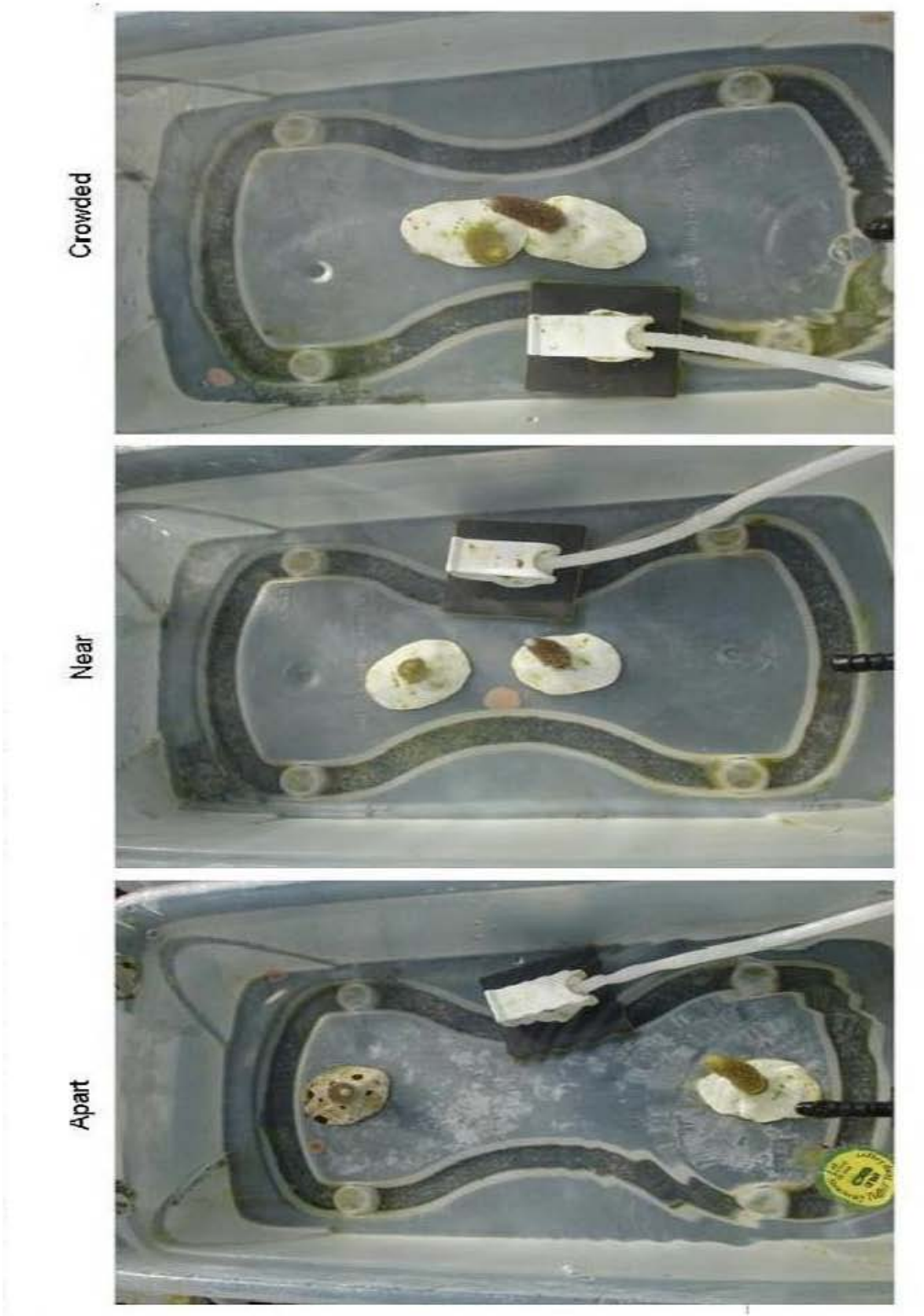
containers within each row were rotated on a weekly basis so that each container received similar exposure over the course of the experiment.

Experimental design

Clonal fragments of each species were exposed to three spacing treatments; Apart, Near, and Crowded. The distances for each treatment were as follows: 'Apart':140mm; 'Near': 33mm; 'Crowded': 8mm. One replicate of each of the three treatments was defined as an experimental unit (Figure 3). Each treatment consisted of one un-branched fragment of *P. cylindrica* and one un-branched fragment of *A. pulchra* in a single container positioned at one of the three spacing distances. The 'Apart' treatment was designed so that corals would have no possibility of growing into contact within the six month period. To determine this distance, I used published growth rates for *P. cylindrica* and *A. pulchra*. For the 'Apart' treatment, growth rates were used a general reference for determining the minimum spacing distance that would prevent contact between fragments throughout the study period. For *Acropora pulchra* Yap and Gomez (1984) projected an annual growth rate of 130 mm. For *P. cylindrica*, Smith (2004) reported a growth rate of 21 mm per year. The 'Near' treatment was designed so that the growth of the corals over a six-month period might result in contact between the two species. This distance was determined by observations I made in the field, where the selected coral colonies were growing directly adjacent to each other. The average distance (30 observations on 15 different colonies) between branches among the coral colonies in situ was 33 mm. The 'crowded' treatment was designed so that the growth of the corals would likely result in physical contact between the two species within two months. This experiment was replicated twelve times, with each experimental unit containing different genotypes of *P. cylindrica* and *A. pulchra*. A coin

toss (using *P. cylindrica* as the ‘reference’) was used to determine the North or South position of each fragment within the container. Experimental units were arranged in a randomized block design.

Figure 3. Experimental unit design; each unit consists of three treatments: Apart, Near, and Crowded.



The Number Crunching Statistical Systems (NCSS) software package will be used to analyze all of the data (Hintze 2001). In all tests, *A. pulchra* and *P. cylindrica* will be analyzed

separately. To meet the assumptions necessary for Analysis of Variance (ANOVA), homoscedacity and normality will be tested using Levene's test and the Shapiro-Wilks W test, respectively. Although ANOVA is tolerant to deviations from these assumptions (Tiku 1971; Glass et al. 1972) in the case where these tests reveal substantial violations in these assumptions, I will use the Box-Cox reference to determine an appropriate transformation to normalize the data. Count data for the number of branches and branch orientation used in ANOVA was transformed using a square root transformation. This experiment was set up as a clonal design (each replicate was represented by a different genotype). Therefore, the potential interaction between clones and treatments must be addressed. The inability to distinguish interaction may result in the inability to conclude that the response from the corals is due to the treatments rather than a predetermined genotypic growth strategy. To elucidate on the potential presence of interaction, I will perform a Tukey's Test for Additivity. Additivity is the assumption that interaction is not present between ANOVA main factors (Table 1). Data used to determine significant interaction between clones and treatments will be obtained from the growth data in the month of June. If interaction is present, data will be Log transformed. In the event that the entire data set cannot be normalized for use in an ANOVA or if substantial interaction between clones and treatments is present, I will use a non-parametric test such as Friedman's Method for Randomized Blocks.

Growth rates for each species did not conform to normality. The greatest influence contributing to non-normality was the data from the last month of the study period. In order to use Repeated Measures ANOVA, and be able to find differences in both treatments and months, I removed the last month of data from the analysis.

Fig 1. Summary of results for Tukeys Test for Additivity

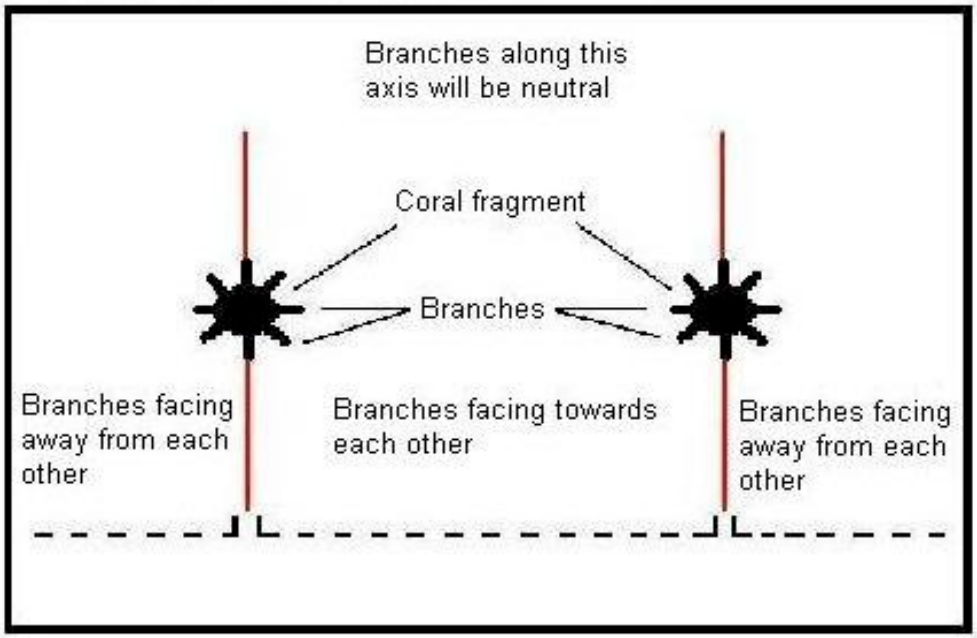
Test	*F**	Critical value (F) (0.05; df = 1,21)	Decision
Linear growth			
Acropora pulchra	1.52	4.32	1.52 < 4.32; No interaction
Porites cylindrica	9.26	4.32	9.26 > 4.32; Interaction present
Basal width growth			
Acropora pulchra	0.38	4.32	0.38 < 4.32; No interaction
Porites cylindrica	1.66	4.32	1.66 < 4.32; No interaction
Linear growth rate			
Acropora pulchra	2.14	4.32	2.14 < 4.32; No interaction
Porites cylindrica	6.58	4.32	6.58 > 4.32; Interaction present
Basal width growth rate			
Acropora pulchra	2.72	4.32	2.72 < 4.32; No interaction
Porites cylindrica	0.8	4.32	0.8 < 4.32; No interaction
Branch number			
Acropora pulchra	2.14	4.32	2.14 < 4.32; No interaction
Porites cylindrica	1.29	4.32	1.29 < 4.32; No interaction
Branch orientation			
Porites cylindrica	12.72	4.32	12.72 > 4.32; Interaction present
Weight			
Acropora pulchra	6.05	4.32	6.05 > 4.32; Interaction present
Porites cylindrica	9.64	4.32	9.64 > 4.32; Interaction present

Hypothesis 1

To test this hypothesis, I measured the total linear and basal width growth and growth rate throughout the study period; total growth (weight of each fragment), counted the number of

branches that developed and the orientation of new branches for each coral fragment at the end of the experiment. To obtain growth rate, measurements for each fragment were taken once per month for six months. Fragment length and basal width were measured in millimeters, using hand-held calipers. Length was measured from the base of the fragment to the tip. It is expected that *Porites cylindrica* will bifurcate at the tip into two or three branches. The tallest branch will be used for the linear growth measurements. Basal width was measured from the point where the fragment meets the base and included any new growth that encrusted over the base. Fragments were weighed in air using a Sartorius analytical balance. Fragments were bleached and placed in the sun to air dry. Prior to weighing, fragments were placed in an oven (low heat) to eliminate moisture. I defined a new branch as any protrusion growing off of the main axis that has a measurable length and direction. Branch orientation was determined by two methods. First, new branches that developed on each clone were tested for uniformity around the axis of the main fragment using Rayleighs Test for Circular Uniformity. The angle of each branch was plotted on an X and Y coordinate graph. Each branch angle was converted into *sine* and *cosine* which was used for the analysis. Rayleighs test generates *z* values which were used in the Two-Factor ANOVA. Second, new branches were categorized as either facing towards or away from the neighbor (Figure 4). Branches growing along the line of separation were not used in the analysis. For each fragment, a ratio was generated: the number of branches facing towards the neighbor / total number of branches. A proportion greater than 0.5 meant the majority of the branches would be facing towards the neighbor. A proportion less than 0.5 meant the majority of the branches would be facing away from the neighbor.

Figure 4. Orientation of new branches was determined by dividing the fragment into two halves; branches growing on a particular 'side' were categorized as either facing towards or away from the neighbor. Branches growing along the axis were neutral.



Data for cumulative growth and growth rate was analyzed using a *Two Factor ANOVA with Repeated Measures on One Factor* (Neter 1996). The first factor was treatment distance (D) constant for the length of the experiment and the second factor (repeatedly measured) was the sampling period (6 months) that data are collected (T). Sphericity is an assumption associated with a repeated measures design. Sphericity is the assumption that the variances of the differences between the repeated measurements are equal. The NCSS package automatically tests for the effects of sphericity using Maulchy's Test for Sphericity and Estimates of Epsilon, and makes corrections using the Greenhouse-Geisser Epsilon adjustments (Hintze 2001). Data for weight, number of branches, and branch orientation (facing towards or away from the neighbor) will be analyzed using a *Two Factor ANOVA Without Replication*. Uniformity of new branches around the axis of each fragment was analyzed using *Rayleigh's test for circular*

uniformity. The first factor was the clones (C) and the second factor was the treatment distance (D). A Tukey-Kramer Post-Hoc test was used to determine significant differences between treatments and a Bonferroni Post-Hoc test was used to determine significant differences between months.

Obstacles associated with this design were the viability of the test subjects throughout the study period, and interference (Carry-over and order effects). This experiment required that all of the subjects that were initially measured remained viable throughout the study period or, at least, that I have a sample size large enough for analysis at the end of the experiment. To address this, I replicated each experimental unit twelve times. Interference comprises both the carry-over and order effect. The carry-over effect can be present in experiments where subjects are exposed to multiple treatments. This effect does not apply here since each subject was exposed to a fixed treatment. Order effect can happen if the subjects are manipulated or exposed to treatments in a non-random order. To ensure that interference (Order effect) was not operating, I randomized the order in which subjects were manipulated during cleaning, measurement taking, and feeding.

Results

Linear Growth

Figure 5 shows the mean monthly cumulative linear growth for *Acropora pulchra* during the 6-month study period. In January, *Acropora pulchra* began to show a difference in cumulative linear growth between treatments, with fragments in the 'Crowded' treatment growing more than fragments in the 'Apart' and 'Near' treatments. By the end of the experiment, fragments in the 'Crowded' treatment had grown significantly more than fragments the 'Apart' treatments (ANOVA, df = 2, 33; F = 3.51; P = 0.0414; Tukey-Kramer Crowded > Apart, @ α .05). A Bonferroni Post-Hoc test (Figure 6a - c) shows the difference in cumulative growth between months for each treatment.

Figure 5. Mean (+/- SD) cumulative linear growth for *Acropora pulchra* in three treatments (Apart, Near, Crowded; n=12 per treatment)

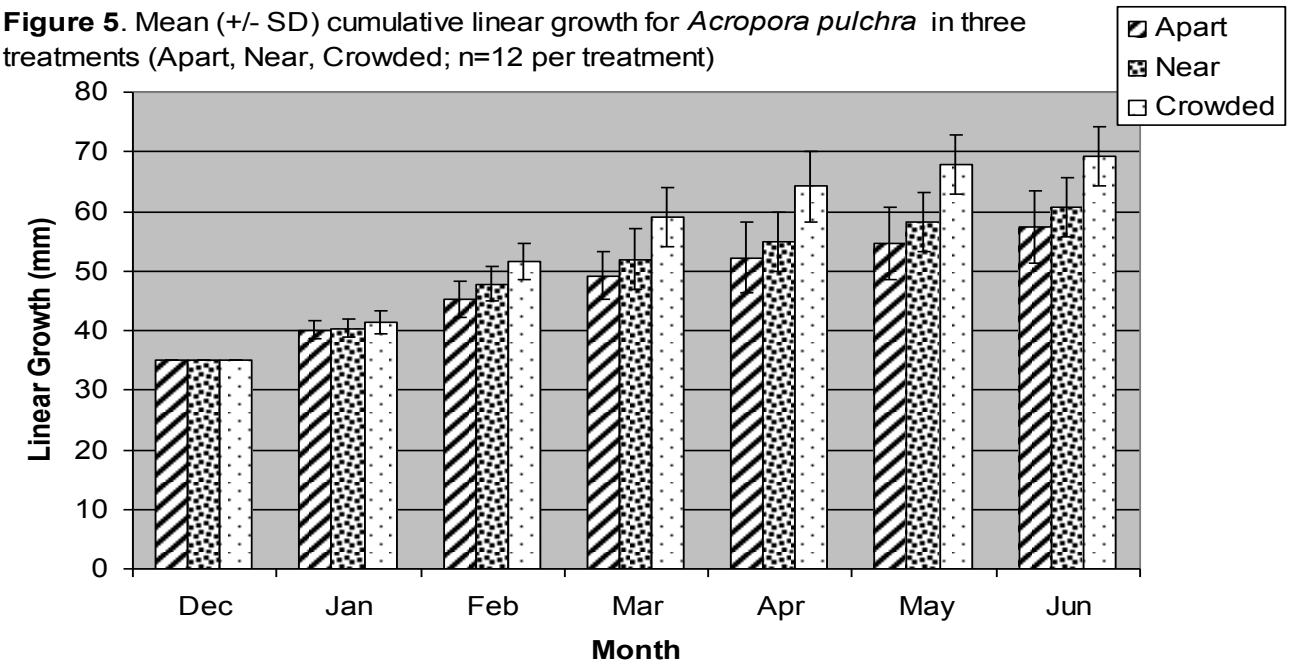
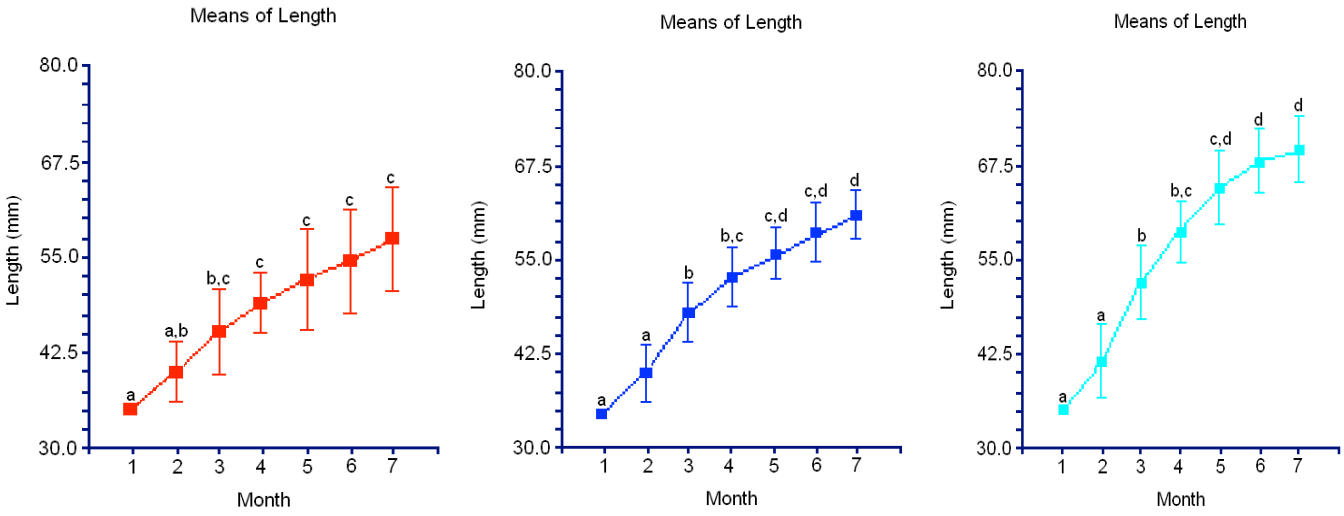


Figure 6a - c. Mean (+/- SD) monthly (30 days) cumulative growth for *A. pulchra* (treatments: a = Apart, b = Near, c = Crowded). Values with different letters were significantly different from each other (P < 0.05; Bonferroni test).

a b c



Growth rates are shown in Figure 7. Although fragment in the 'Crowded' treatment had the highest amount of variability, there was a significant difference between treatments (ANOVA df = 2, 33; $F = 9.52$; $P < 0.0005$; Tukey-Kramer: Crowded > Apart, Near, $\alpha = .05$). Figure 8a - c shows the difference in growth rate between months for each treatment. Initial growth rates were higher than rates towards the end of the experiment with fragments in the 'Crowded' treatment showing the highest growth rate. However, in the last month of the experiment, fragments in the 'Crowded' treatment showed the lowest growth rate.

Figure 7. Monthly (30 days) linear growth rate (+/-SD) for *Acropora pulchra* in three spacing treatments (Apart, Near and Crowded; n = 12 per treatment).

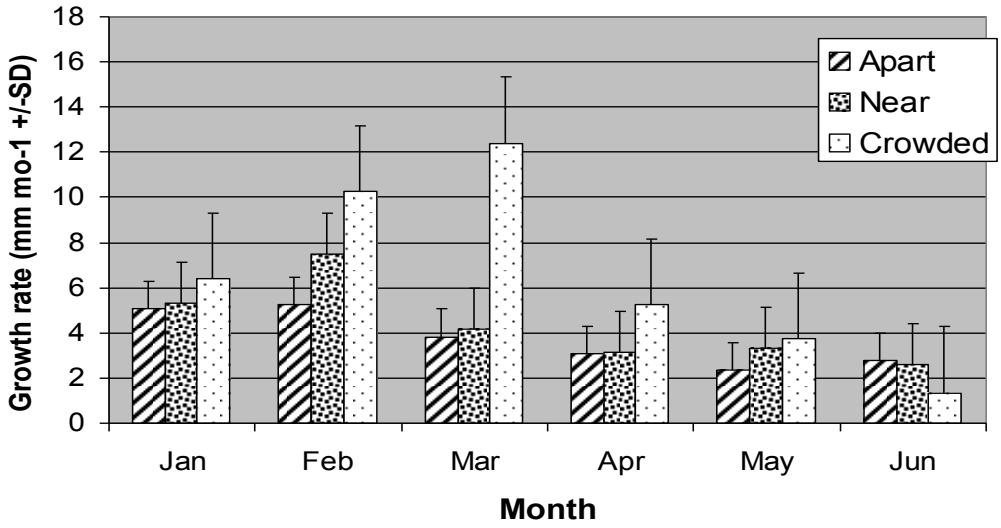
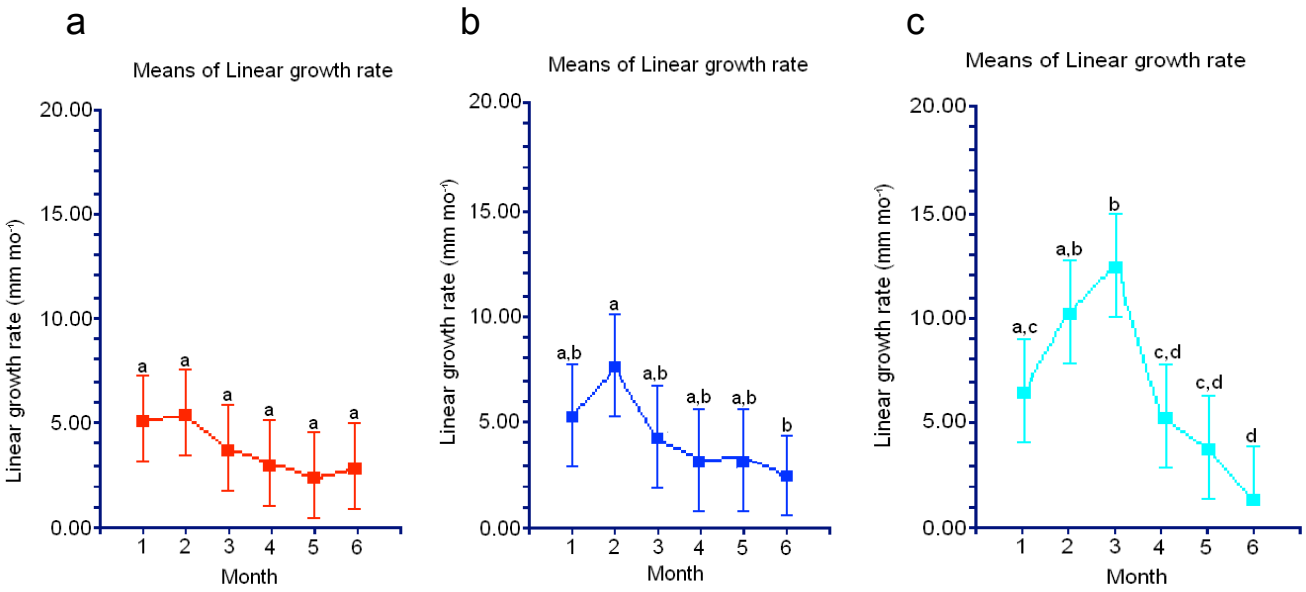


Figure 8a - c. Mean (+/- SD) monthly (30 days) growth rate for *A. pulchra* (treatments: a = Apart, b = Near, c = Crowded). Values with different letters were significantly different from each other ($P < 0.05$; Bonferroni test).



Porites cylindrica showed no significant difference in total cumulative linear growth or growth rate between treatments (Fig. 9, ANOVA, df = 2, 33; $F = 1.05$; $P = 0.3621$; Fig. 10, ANOVA df = 2, 33; $F = 0.68$; $P = 0.5153$). Although there was no significant difference among treatments, there was a difference in cumulative growth between months (Figure 7a - c) with the least amount of growth occurring in the 'Crowded' treatment. Figure 8a - c shows the difference in growth rate between months for each treatment during the 6-month study period.

Figure 9. Mean (+/- SD) cumulative linear growth for *Porites cylindrica* three treatments (Apart, Near, Crowded; n=12 per treatment)

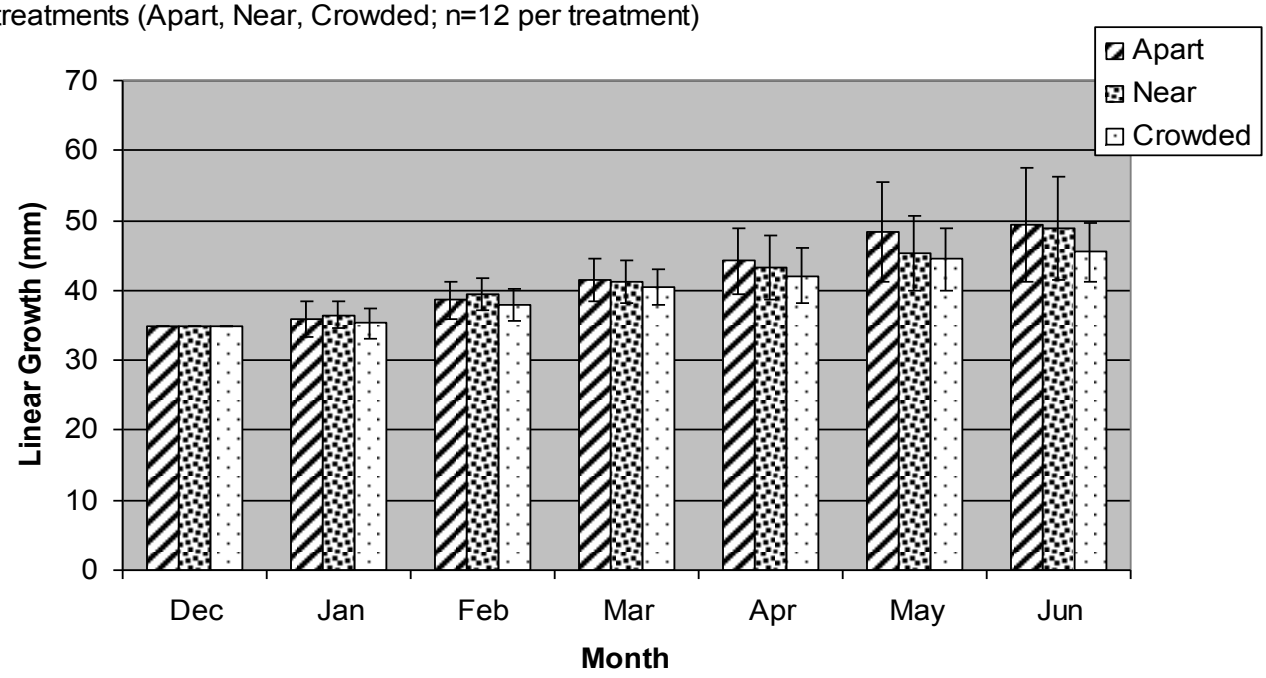


Figure 10. Monthly (30 days) linear growth rate (+/-SD) for *Porites cylindrica* in three spacing treatments (Apart, Near and Crowded; n = 12 per treatment).

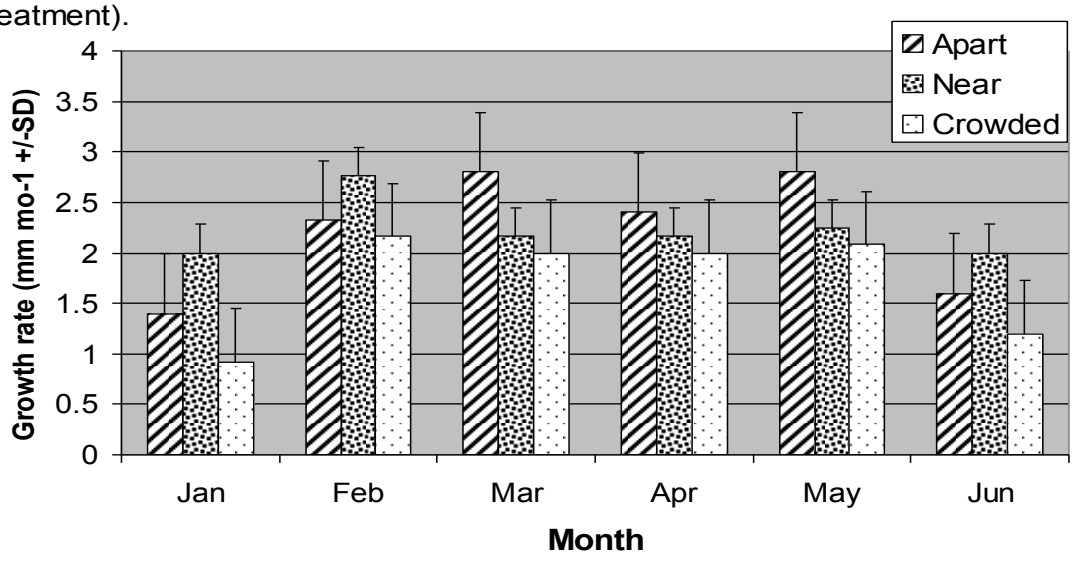


Figure 11a - c. Mean (+/- SD) monthly cumulative growth for *P. cylindrica* (treatments: a = Apart, b = Near, c = Crowded). Values with different letters were significantly different from each other ($P < 0.05$; Bonferroni test).

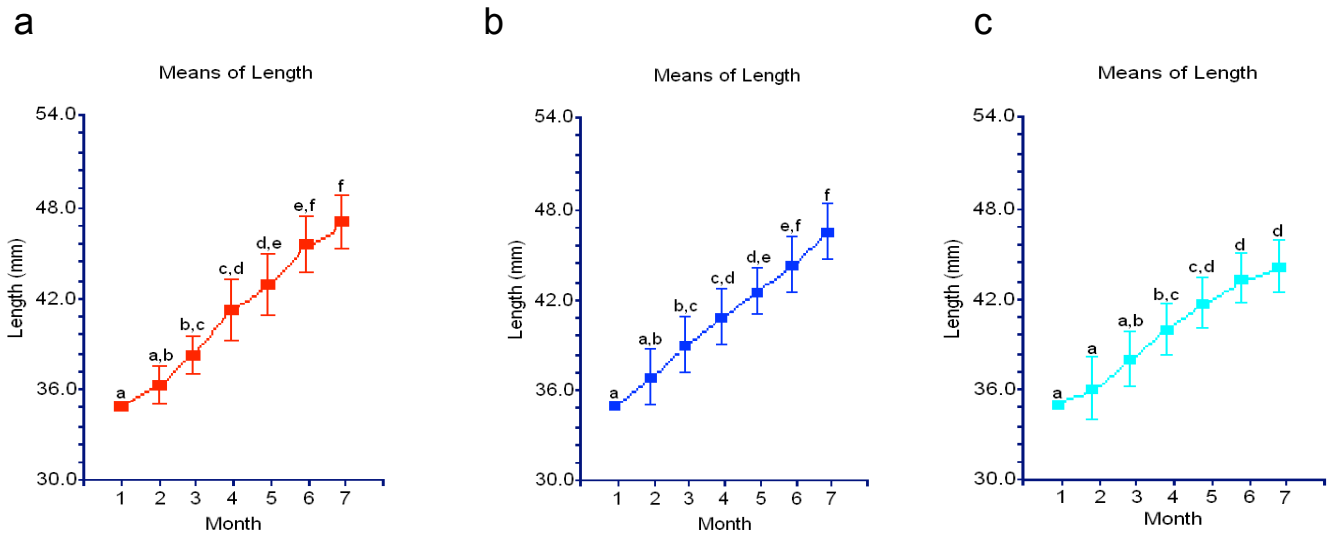
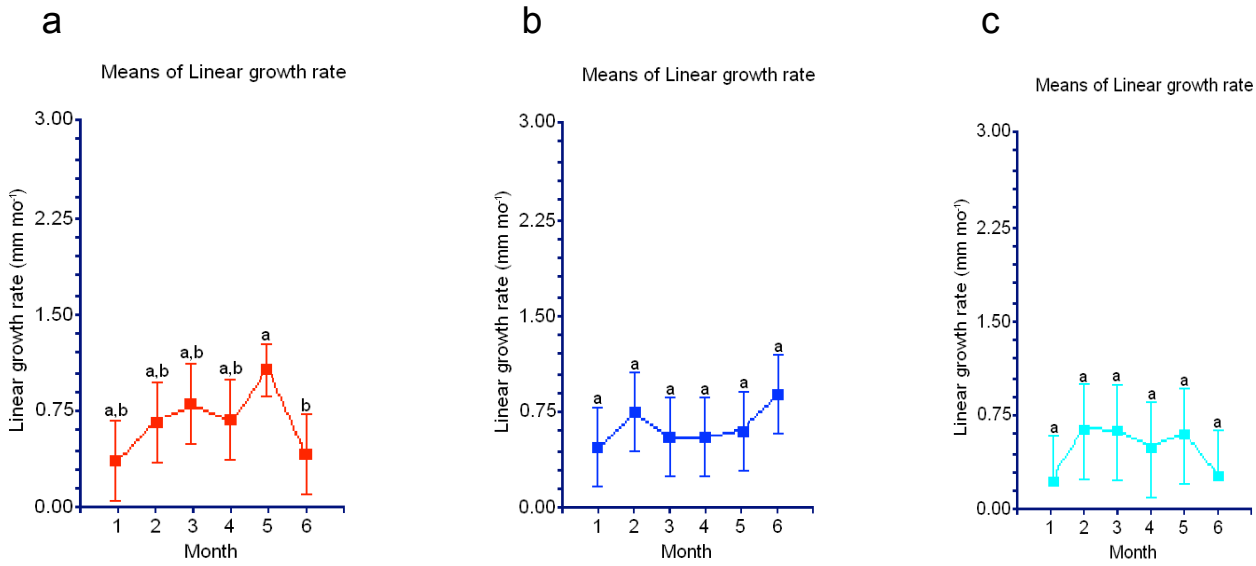


Figure 12a - c. Mean (+/- SD) monthly growth rate for *P. cylindrica* (treatments: a = Apart, b = Near, c = Crowded). Values with different letter were significantly different from each other (P < 0.05; Bonferroni test).



Basal width growth

Figures 13 and 14 each show the mean monthly cumulative basal width growth for *Acropora pulchra* and *Porites cylindrica* during the 6-month study period. Although there were differences in linear growth, there were no differences in basal width growth between treatments for each species (ANOVA, *A. pulchra*: df = 2, 33; *F* = 1.34; *P* = 0.2761; *P. cylindrica*: df = 2, 33; *F* = 0.46; *P* = 0.6352). Throughout the study period, basal growth increased. Likewise, growth rates were not significantly different between treatments for either species (Fig 15, ANOVA, *A. pulchra*: df = 2, 33; *F* = 0.14; *P* = 0.8701; Fig 16, *P. cylindrica*: df = 2, 33; *F* = 0.80; *P* = 0.4567). However, there were differences in growth rate between months for each species. Basal width growth rate for *A. pulchra* was the highest during the first 3 months (Jan – Mar) but showed a decline in the subsequent months. Basal width growth for *P. cylindrica* varied between treatments with no apparent trend.

Figure 13. Mean (+/- SD) cumulative basal width growth for *Acropora pulchra* in three treatments (Apart, Near, Crowded; n=12 per treatment)

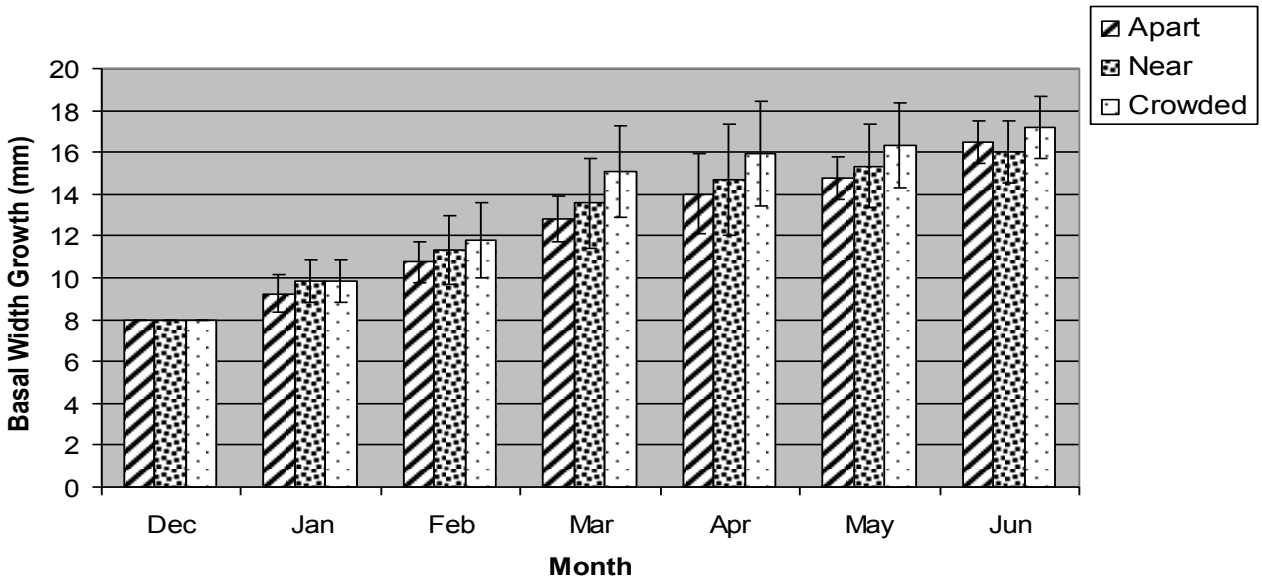


Figure 14. Mean (+/- SD) cumulative basal width growth for *Porites cylindrica* in three treatments (Apart, Near, Crowded; n=12 per treatment)

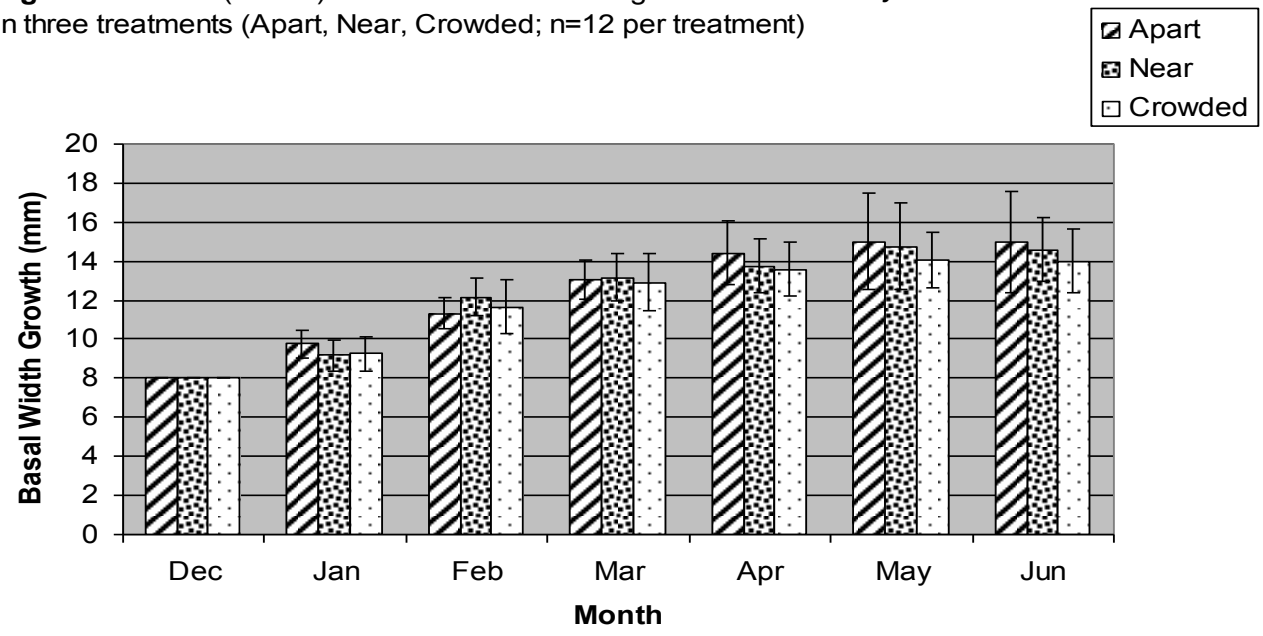


Figure 15. Monthly (30 days) basal width growth rate (+/- SD) for *Acropora pulchra* in three spacing treatments (Apart, Near and Crowded; n = 12 per treatment).

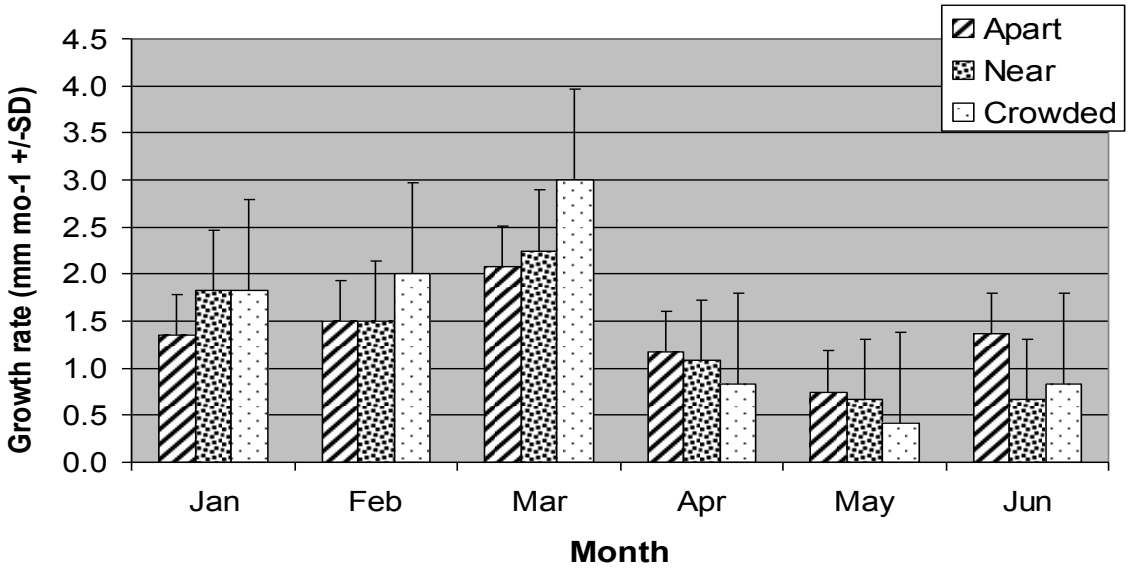
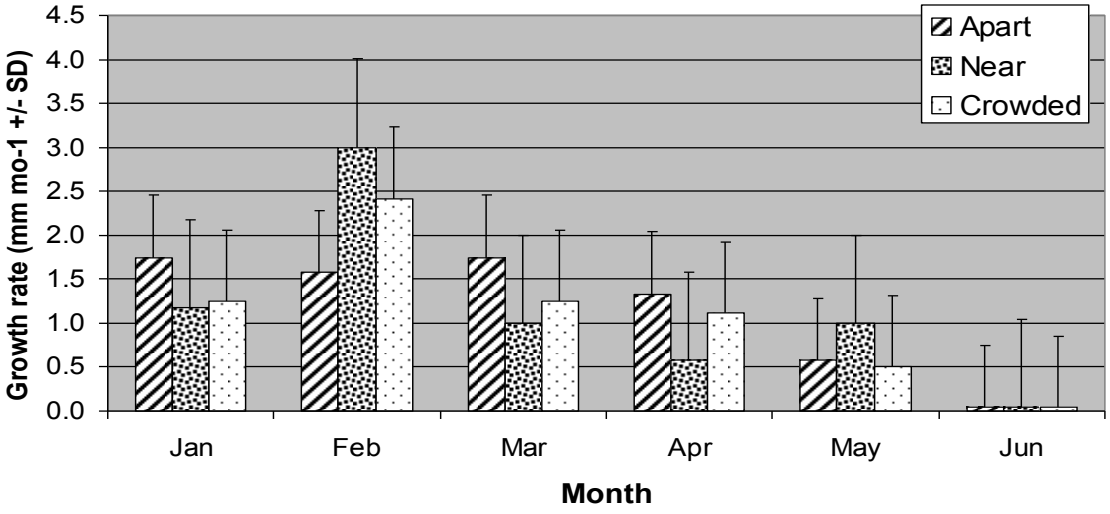


Figure 16. Monthly (30 days) basal width growth rate (+/-SD) for Porites cylindrica in three spacing treatments (Apart, Near and Crowded; n = 12 per treatment).



Branch number

Figure 17 shows the mean number of new branches that developed for *A. pulchra* at the end of the experiment. Although *A. pulchra* did not branch extensively, there was a significant

difference in the number of new branches between the treatments (ANOVA, df = 2, 33; *F* = 2.70; *P* = 0.0823). While fragments in the 'Near' treatment showed an increase in branch development over fragments in the 'Apart' treatment, the number of branches was highest in the 'Crowded' treatment. Further, although no measurements were taken on the length of individual branches, new branches developed sooner on fragments in the 'Crowded' treatment. As a result, new branches were longer than new branches that developed on fragments in the 'Near' treatment. *P. cylindrica* branched extensively in the 'Near' and 'Apart' treatments (Figure 18), with a significant difference in the number of new branches between the treatments (ANOVA, df = 2, 33; *F* = 3.72; *P* = 0.0350; Tukey-Kramer, Apart > Crowded, *P* = 0.05).

Figure 17. Mean (+/- SD) number of branches for *Acropora pulchra* in three treatments (Apart, Near, Crowded, n=12 per treatment)

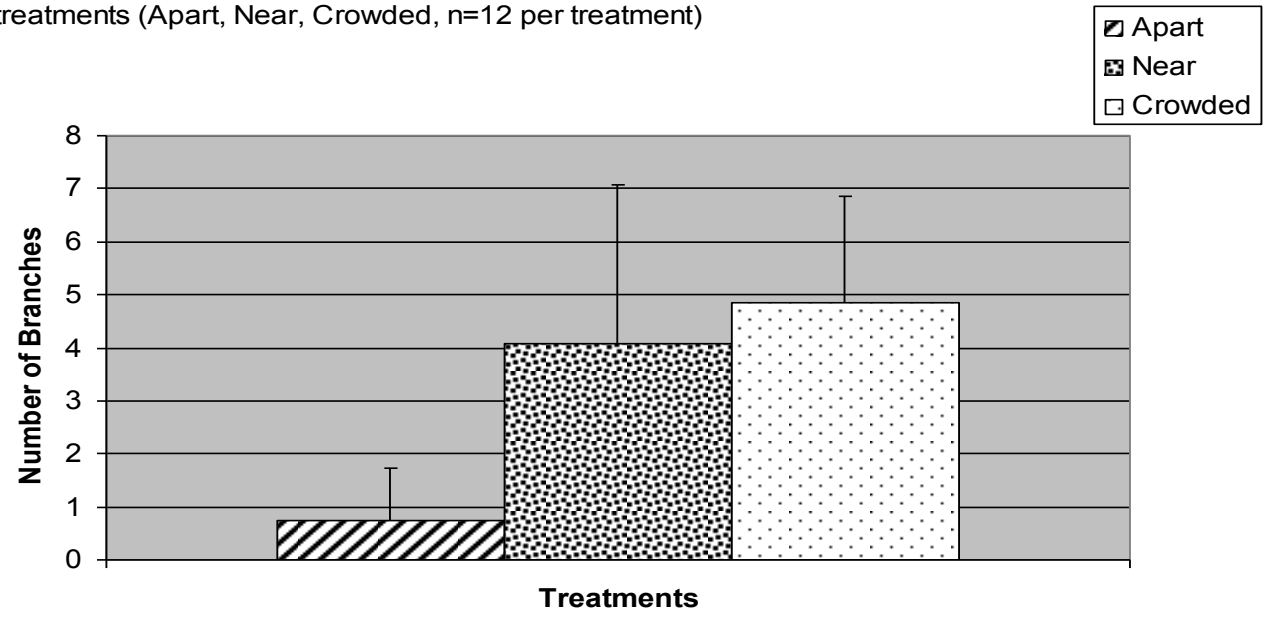
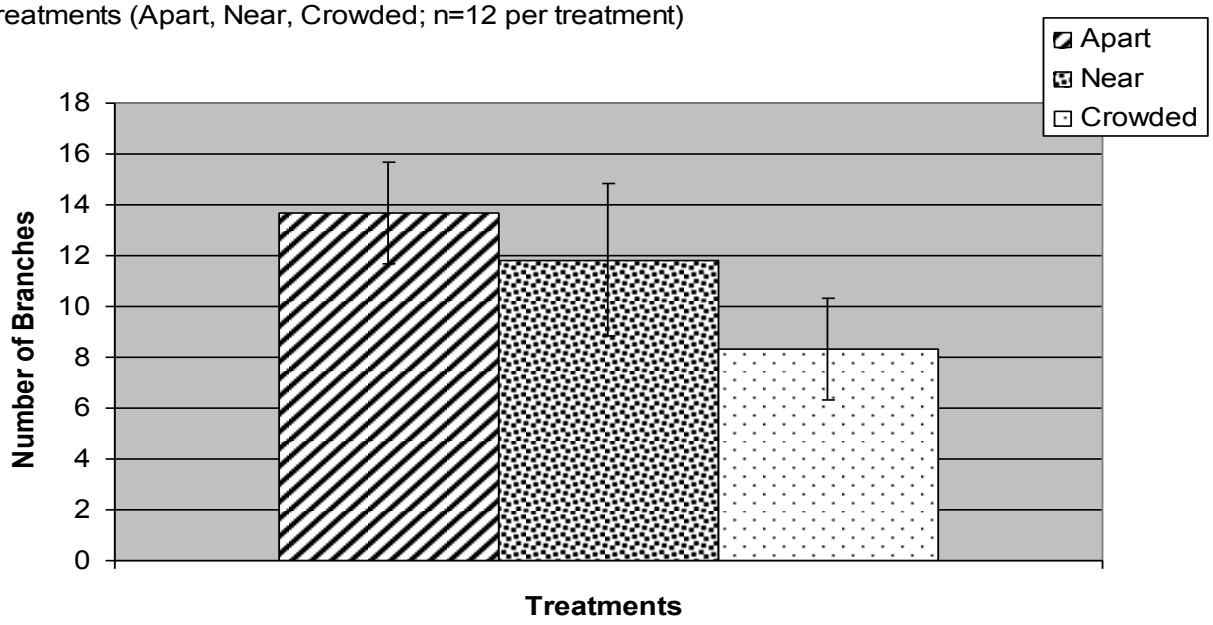


Figure 18. Mean (+/- SD) number of branches for *Porites cylindrica* in three treatments (Apart, Near, Crowded; n=12 per treatment)



Although both species showed significant differences in the number of branches between 'Crowded' and 'Apart' treatments, responses were opposite. *A. pulchra* showed the highest number of branches in the 'Crowded' treatment where *P. cylindrica* showed the highest number of branches in the 'Apart' treatment.

Branch orientation

Due to the small sample size (in many cases the number of new branches ≤ 3), branch orientation patterns for *Acropora pulchra* could not be discerned. However, new branches that grew on fragments in the 'Crowded' treatment predominantly grew near the surface of the water. Although new branches were abundant on the fragments at the end of the 6-month study period, there was no significant difference in the orientation of new branches for *P. cylindrica* (ANOVA on Rayleigh's Test for Circular Uniformity, df = 2, 33; $F = 1.21$; $P = 0.3097$).

Table 2 presents the mean percent of branches orienting either towards or away from the neighbor.

Table 2. Orientation (towards or away from neighbor) of new branches. Percent based on the proportion of branches orienting towards the neighbor / total number of branches. A proportion > 0.50 = most branches facing towards the neighbor. A proportion < 0.50 = most branches facing away from the neighbor.

	Treatment		
	Apart (%)	Near (%)	Crowded (%)
Acropora pulchra	40 (SD +/- 41.08) (n = 5)	31 (SD +/- 25.01) (n = 6)	36 (SD +/- 33.02) (n = 10)
Porites cylindrica	50 (SD +/- 15.83) (n = 12)	51 (SD +/- 7.84) (n = 12)	41 (SD +/- 16.51) (n = 11)

Total growth: weight

Figures 19 and 20 each show the mean total weight increase for *A. pulchra* and *P. cylindrica*. Although both species grew significantly differently between treatments (*A. pulchra*; ANOVA, df = 2, 33; $F = 5.03$; $P = 0.0124$; *P. cylindrica*; df = 2, 33; $F = 3.77$; $P = 0.0336$), the weight increase for *A. pulchra* was significantly higher in the 'Crowded' treatment than in the 'Apart' treatment (Tukey-Kramer MCP, Apart < Crowded, $\alpha = 0.05$). This is consistent with previous results. Likewise, *P. cylindrica* fragments in the 'Apart' treatment were significantly heavier than in the 'Crowded' treatment (Tukey-Kramer MCP, Apart > Crowded, $\alpha = 0.05$). This, too, is consistent with previous results. The difference in total weight between the treatments shows that, although their growth strategies were different (i.e. linear growth for *A. pulchra* and branch development for *P. cylindrica*), each species showed a growth response to the close proximity of their neighbor.

Figure 19. Mean (+/- SD) total weight increase for *Acropora pulchra* in three treatments (Apart, Near, Crowded, n=12 per treatment)

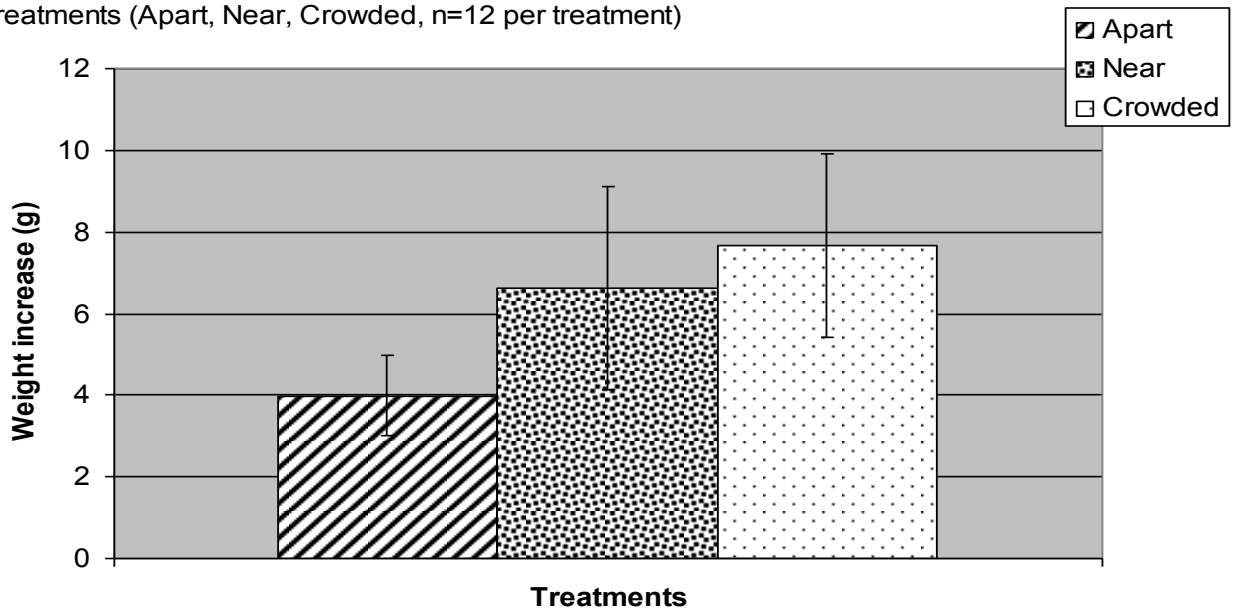
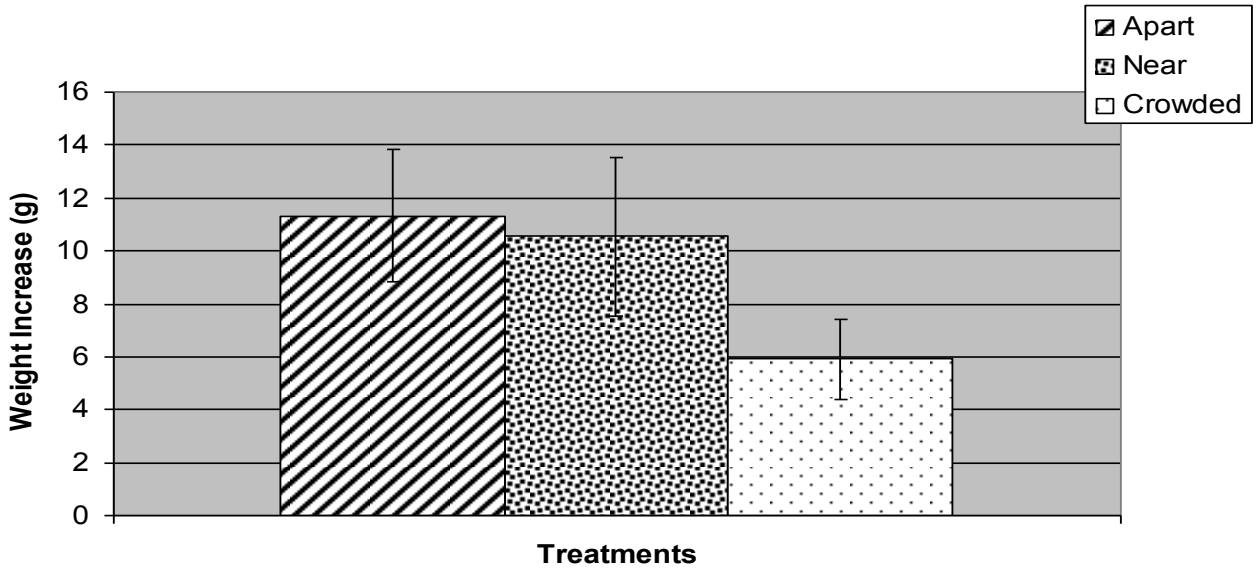


Figure 20. Mean (+/- SD) total weight increase for *Porites cylindrica* in three treatments (Apart, Near, Crowded; n=12 per treatment)



Summary

Results for all of the tests are summarized in Table 3. Both *Acropora pulchra* and *Porites cylindrica* showed a consistent pattern of growth among clones and treatments. *Acropora pulchra* grew in length, but did not branch extensively. Conversely, *P. cylindrica* did not significantly growth in length, but added a significant amount of new branches to the main fragment. Although both species added growth to the base there were no significant differences between treatments. The weight gain for both species reflected their difference in overall growth.

Table 3. Summary of results for *A. pulchra* and *P. cylindrica*

Test	Decision
Linear growth	
Acropora pulchra	Significant difference (Crowded > Apart)
Porites cylindrica	No significant difference
Linear growth rate	
Acropora pulchra	Significant difference (Crowded > Apart)
Porites cylindrica	No significant difference
Basal width growth	
Acropora pulchra	No significant difference
Porites cylindrica	No significant difference
Basal width growth rate	
Acropora pulchra	No significant difference
Porites cylindrica	No significant difference
Weight	
Acropora pulchra	Significant difference (Crowded > Apart)
Porites cylindrica	Significant difference (Apart > Crowded)
Branch number	
Acropora pulchra	Significant difference (Crowded > Apart)
Porites cylindrica	Significant difference (Apart > Crowded)
Branch orientation	
Acropora pulchra	N/A
Porites cylindrica	No significant difference

Discussion

This study showed that culturing *Acropora pulchra* and *Porites cylindrica* at three spacing distances from each other resulted in different responses manifested in phenotypic growth and morphology. Growth patterns for *Porites cylindrica* were directed towards the development of branches and growth patterns for *Acropora pulchra* were directed towards linear extension with branch development at the tips. Although I predicted that some of the growth patterns and competitive interactions for each species would be consistent with previous findings, the fastest growth rates of *Acropora pulchra* in response to direct contact with *P. cylindrica* was not predicted. Previous work has demonstrated that corals engaged in physical contact would show reduced growth rates (Rinkevich and Loya 1985; Tanner 1997).

Although both *Acropora pulchra* and *Porites cylindrica* are similar in branching morphologies and colony size, their growth rates and competitive strategies are significantly different. *Acropora pulchra* colonies grow quickly to establish large, often dominating thickets on shallow reef flats (Wallace 1999; Connell et al. 2004). Annual linear extension rates can exceed 180 mm (Yap and Gomez 1984). Fast growth in many species of *Acropora* has been shown to be a survival strategy (Soong and Chen 2003) and a competitive strategy; using both direct and indirect mechanisms (Potts 1976; Baird & Hughes 2000). Although allocating energy for fast growth can provide a competitive edge, the ability to repair damaged areas and adapt to changes in environmental parameters can be negatively affected (Meesters and Bak 1996; Baird and Marshall 2002). Further, Jokiel and Coles (1990) found a strong correlation between corals that have high respiration rates, such as fast growing *Acropora*, and susceptibility to

thermal stress. In contrast to *A. pulchra*, colonies of *Porites cylindrica* have a slower growth rate (20 mm/yr; Smith 2004). *Porites sp*. are usually subordinate to a variety of other corals as demonstrated by their lack in the development of aggressive mechanisms (Sheppard 1979; Rinkevich & Sakai 2001). However, in some habitats they can be the most common species (Shepard 1979; Veron 2000). It has been suggested that their success on the reef is due to their ability to acclimatize to changes in environmental parameters such as severe fluctuations in temperature and bleaching events (Coles and Fadlallah 1990; Baird and Marshall 2002). Jones et al. (2000) have suggested that *Porites sp*. can withdraw their polyps deep into the corallites, thus providing the polyps with higher amounts of shading. This would allow for more protection against direct sunlight which can contribute to thermal stress. In transplantation experiments, Clark and Edwards (1995) showed that Poritids had the highest rates of survival although growth rate was the slowest. This is in contrast to *Acropora hyacinthus* (same study) which showed the highest growth rate and highest mortality. Therefore, while colonies of *A. pulchra* grow quickly, they appear to possess short term competitive advantages directed towards the ability to dominate other species of coral, whereas *P. cylindrica* may invest resources into strategies that are better able to cope with changes in environmental parameters that may affect their long-term survival.

In this experiment, growth response of both *Acropora pulchra* and *Porites cylindrica* due to fragmentation was consistent with previous findings (Soong & Chen 2003; Smith 2004). First, Clark and Edwards (1995) found that basal growth stabilized growing colonies and was important to later growth and survival of transplanted fragments. In all treatments, basal growth was observed with no differences between treatments. Growth rates were higher in the first

three months which shows that both species were attempting to stabilize on the substrate. Second, the observed reduced growth rates relative to that of parent colonies on the reef were most likely due to transplant stress (Yap and Gomez 1984; Raymundo 2001). In this study, colonies were fragmented and relocated to the laboratory environment. In treatments where neither coral physically interacted with its neighbor, I observed growth rates and morphology similar to those of transplanted fragments on the reef (Custodio and Yap 1997; Soong and Chen 2003). Finally, by the third month, 11 out of 12 fragments in the 'Crowded' treatment had grown into physical contact of each other. This elicited a competitive response in which *A. pulchra* was dominant over *P. cylindrica.* This was apparent from tissue loss at the area of contact and reduced growth in *P. cylindrica*. These responses were not apparent in treatments where no physical contact was observed.

Acropora pulchra

In treatments where no physical contact occurred, growth patterns of *Acropora pulchra* were consistent with previous work (Yap and Gomez 1981; Soong and Chen 2003). However, the high growth rates among the fragments engaged in physical contact with *P. cylindrica* was not predicted. Previous work has shown that fast growth of *A. pulchra* would pre-empt space by overtopping slower growing corals (Lang and Chornesky 1990; Baird and Hughes 2000). The physical proximity of *P. cylindrica* could have instigated the faster growth recorded for *A. pulchra* in the 'Crowded' treatment however, in cases where *Acropora* was in physical contact with another coral, growth rates were found to be reduced (Tanner 1997). Further, because of the development of mechanisms that enabled *A. pulchra* to dominate *P. cylindrica*, I expected that *A. pulchra* would show a reduction in growth as energy was invested into developing and

maintaining such mechanisms (Chornesky 1989). In the ‘Crowded’ treatment, the main fragments initially showed the fastest growth rate and produced very few branches. However, by the third month, two things became apparent. First, the main fragments had reached the surface of the water and second, there was physical contact between the two species. At that time, I noticed a change in growth patterns. Linear growth rate declined and new branch development at the top of the fragment started to increase. The reduction in linear growth rate, becoming the slowest among the treatments in the final month, was probably due to the limit set by reaching the water level. While branching may be attributed to the restriction in the ability to grow in length, the increase in branching at the tip of the fragments in the ‘Crowded’ treatment suggested that contact with *P. cylindrica* may have triggered a competitive response in *A. pulchra*. In the ‘Near’ treatment many of the fragments grew to reach the surface of the water but within the study period did not branch as extensively as fragments in the ‘Crowded’ treatment.

While it has not been shown that corals are able to digest other corals for nutritional requirements, it is well known that they are predators and will eat a variety of reef organisms (Goreau et al. 1971). It has also been shown that coral mucus, which contains high levels organic matter, is consumed as food by many benthic organisms such as (Wild et al. 2004). Further, Ferrier-pages et al. (2004) observed that colonies of *Stylophora pistillata* would continue to consume prey items as long as they were available, thus never reaching a point of being saturated. Therefore, although I did not determine if *A. pulchra* was feeding directly on the tissue of *P. cylindrica*, or on the mucus sheets which *P. cylindrica* are known to create (Kato 1987), or as a result of the tissue loss to *P. cylindrica*, was exposed to higher amounts of

Artemia fransiscana, it is possible that fragments of *A. pulchra* in the 'Crowded' treatment were exposed to greater amounts of nutritional sources.

The increase in branch development in the 'Crowded' treatment may indirectly be further evidence that fragments may have had additional nutritional resources. Soong and Chen (2003) found that branches developed quicker on longer fragments. In this case, overtopping as an indirect mechanism to dominate neighboring corals is most likely a function of available resources and growth morphology; not a direct response to the presence of the competitor.

Porites cylindrica

Growth patterns of *Porites cylindrica* in all of the treatments were consistent with growth and morphology found in previous work (Custodio and Yap 1997; Smith 2004). In treatments where no interaction was observed there was an increase in growth rate and branch development. In the 'Crowded' treatment where physical contact with *A. pulchra* occurred, *Porites cylindrica* showed a significant reduction in linear growth rate and branch development. These results suggest that being physically subordinate to *A. pulchra* can have a negative effect on growth. Similar to *A. pulchra*, the least amount of linear growth occurred at the end of the study period. Unlike *A. pulchra*, fragments did not reach the water surface and, therefore, the limited linear growth was not due to that particular growth barrier. Rather, fragments in the 'Crowded' treatment were severely damaged by the physical contact and seemed to no longer accumulate new growth. Even though fragments in the other treatments continued to grow longer, they appeared to direct most of the new growth into the development of new branches. Branches did not show a pattern of orientating either towards or away from *A. pulchra*,

however, in the ‘Near’ treatment branches that grew into contact with *A. pulchra* subsequently experienced tissue damage at the point of contact. Rinkevich and Loya (1983) suggested an allelopathic mechanism was at play when they showed that subordinate colonies of *Stylophora pistillata* grew away from the dominant colony, prior to any signs of physical contact. This was not observed in our experiment and would suggest that *P. cylindrica* may not be able to detect the presence of *A. pulchra* until it comes into physical contact. While no measurements where made on the growth rate of individual branches, no further growth was observed on those branches that had made contact with *A. pulchra*. The experiment was terminated prior to determining if new branches would have followed a new pattern of orientation once they came into direct contact with *A. pulchra*.

Morphological plasticity has been shown to exist in many species of corals (Bruno and Edmonds 1997; Muko et al. 2000). Todd et al. (2004) showed that changes in environmental conditions can cause variation in growth and morphology among conspecifics. In this experiment, environmental conditions were held constant to determine if the neighbor had an effect on growth. While the results showed that growth and morphology were influenced by the neighbor, clones in all treatments and both species exhibited no observable difference in their phenotypic response to the varying distances of their neighbor (i.e. responses from all of the clones in any of the treatments were similar). As shown with *Galaxea fascicularis* (Pavia 2004), this suggests that their responses are genetically fixed.

Currently, coral farmers believe coral health and growth are optimized when they are spaced away from each other and grown in tanks containing similar species (Delbeek 2001). However,

I have shown that the careful attention to spacing distances and the poly-culture of different corals can result in higher growth rates. Spacing fragments, either away from a neighbor to inhibit physical contact, or with physical contact to promote a competitive response can be a cost effective way to increase the growth rate and optimize culture tank space. However, financial sustainability in many coral farms requires that all of their corals be healthy in order to increase the number of marketable corals. Therefore, the increase in growth at the expense of another coral colony may not be desirable. Although the exact mechanism for the increased growth found in this study has not been identified, it was most likely the subordinate coral that provided the extra nutrition. Land based coral farms may be able to achieve similar results if they are able to provide constant food additions; however, this is not cost effective. One possible scenario could be the growth of a less marketable coral species to act as a donor colony for fragments that may be used to promote a competitive response in corals that have high market values. Further, the subordinate coral may take the place of food additions, thus reducing the labor and costs associated with live food supplementation.

An indirect result from this experiment is the response of fragments upon reaching the water surface. In the aquarium trade, corals that have extensive branching are more marketable (Borneman Pers comm.). Since extensive branching happened once the fragment reached the water surface, this may be a way to instigate branch development. The combination of more resources and shallow water levels may further reduce the amount of time for grow out at the facility.

These conclusions also have significant relevance to reef restoration efforts. Although the end-use of fragments used for restoration differs from that of corals cultured for the aquarium trade, grow-out methods for the development of potential transplants and donor colonies are similar. The test subjects used in this experiment can further benefit restoration programs, as both *A. pulchra* and *P. cylindrica*, and similar species, are widely used in this capacity (Yap and Gomez 1981; Soong and Chen 2003; Raymundo 2001). Survival of transplanted corals is usually low due to the stress associated with fragmentation, transplantation, and acclimation to the new location (Harriott and Fisk 1988; Yap et al. 1992; Edwards and Clark 1998). To help overcome this, new techniques for transplantation have included an acclimation period and more complete grow-out of fragments in ocean or land-based nurseries prior to placement at the restoration site (Clark and Edwards 1995; Bowden-Kirby 2001). Recently, conservation programs have developed permanent nurseries that house a number of parent colonies (Bowden-Kirby 2001). Rather than harvesting fragments from healthy reefs, fragments are donated from the parent colony grown in a 'captive' environment. In this scenario, the number of new fragments available for transplantation depends on the growth rates of the parent colonies. In either of these cases, the optimal spacing and poly-culture of coral species would lead to faster growth rates and a greater number and diversity of corals available for reef rehabilitation efforts. Further, corals fragmented from parent colonies grown in nurseries have the potential to remove harvesting pressure from healthy donor colonies on the reef.

While this study demonstrated that the distance between two species of coral cultured together can have an affect on growth and morphology, it is clear that further investigation into the mechanisms that caused the increase in growth for *A. pulchra* and the long-term effects on

ploy-cultured corals is required. This experiment is the first step towards refining culturing techniques which will ultimately lead towards the reduction of harvesting wild stock corals for the aquarium trade as well as increasing the survivorship of corals transplanted for reef restoration programs.

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Appendices

Appendix 1. Detailed description of water table design and set-up

Two water tables (Methods, Figure 1) of similar height and size were placed side by side in direct sunlight on the North Lanai at the University of Guam Marine Laboratory. Each water table also has a hinged / removable cover that is made of clear, acrylic and is able to block ultraviolet light from entering the containers. This cover prevents rainwater from entering the containers and potentially disrupting the salinity levels, which may otherwise prove fatal to the fragments. Adjacent to the tables, two main one inch seawater lines were installed; one that is fed by seawater coming directly from the reef flats in Pago Bay and another that is fed by well-water pumped from approx 50' below ground. Both of these lines are joined into a common one inch line. Downstream from this unison, there are two mechanical filters (Pentair Aquatics AF-94, twenty nine inch filters), arranged in parallel, which filtered out large sediment in the seawater lines. The line that flowed out from the filters was reduced to a half inch line which divided into two lines that delivered seawater to both water tables. Each line leading up to the water tables was equipped with a ball valve to allow for each water table to be adjusted or shut off (during feeding) independent of the water flow to the other table. On the opposite side of the tables, the air supply was a half inch line connected to the Marine Lab main air source. The lines that distributed air to each of the tables were equipped with a ball valve that allowed each table to be shut off from the air supply (during feeding) independent of the other table.

Seawater and air manifolds were constructed to evenly distribute seawater and air into each container. One air source and two seawater sources were supplied to each container. Valves on the air manifold allowed for adjustments so that an even amount of aeration was distributed to all containers. The air source into each container was via 3/16'' tubing. Each airline tube that entered the containers was outfitted with a ratchet style clamp attached to a 10cm by 10cm ceramic tile which acted as a weight to keep the airline submerged underwater. Valves on the seawater manifold allowed for adjustments to the seawater flow to ensure even distribution among the containers. The seawater source that fed each container was via one-eighth inch nozzle attached to the seawater manifold. Nozzles were located at long ends of each container. Prior to the beginning of the experiment, the flow rate for each nozzle on the seawater manifold was measured. Measurements were made by using a 100ml beaker and recording the time it took, in seconds, for each nozzle to fill the beaker to the 80ml mark. ANOVA for flow rates can be found in Appendix, 4M. Adjustment of valves both locally (affecting each row of containers within the table) and to the entire manifold (affecting the flow to each manifold on the East and West tables) were enough to keep all of the water flow rates within a range of fifteen percent from each other.

Appendix 2. Detailed description of container and epoxy base design

Each container held five liters of seawater. At the long ends of the container two, ¾" overflow holes were drilled near the top of the container. Two more holes, measuring 3/16" in diameter were drilled at the same level and near the three quarter inch holes to accommodate the airline tubing. To maintain exact distances throughout the study period, each container was designated as either the 'Apart', 'Near' or, 'Crowded' and pre-determined distances were marked off inside. Size #2 tile spacers were glued (using Super Glue designed for plastic) into the appropriate location. Containers were placed in the flow through seawater system to condition them prior to the beginning of the experiment. The epoxy bases were molded using a two-part epoxy that is not reactive in seawater (Delbeek and Sprung 1996). Similar sized pieces of the epoxy were sliced off and molded with a flat bottom, rounded edges and a curved surface. After mixing the two parts of the epoxy, a tile spacer matching the tile spacers glued to each container was embedded in the bottom of the epoxy. After the epoxy base set (dried), the tile spacer was removed, leaving behind an indent in the form of the tile spacer. This created an imprint so that epoxy base could mate together with the container. This allowed each fragment to stay in the exact position while water and air flow through the containers. This also ensured that exact positions were maintained when fragments were removed and replaced during cleaning and measurements. Fragments were embedded in the top part of the epoxy base

and pin holes reflecting the replicate number (numbered 1 through 12) were added for individual identification. To further elucidate what clone was used for each treatment, a line was scratched into the base, near the pinholes, for the fragment designated as the ‘Apart’ treatment. Fragments designated as the ‘Crowded’ treatment was offset within the base to ensure that the distance of 8 mm was met.

Appendix 3. Tukey's test for additivity. The following tables correspond with the summary; Table 2, page 19

Appendix 3a. Tukey's test. Cumulative linear growth for *Acropora pulchra.*

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	3336.89	1112.3	1.52	4.32
B(A): Clone	11	903.72	75.31		
Error	22	940.28	63.56		
Total	35	5180.89			

* Term significant at alpha = 0.05

Appendix 3b. Tukey's test. Linear growth rate for *Acropora pulchra*.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	4.68	1.56	2.14	4.32
B(A): Clone	11	0.9	0.07		
Error	22	7.93	0.73		
Total	35	13.51			

* Term significant at alpha = 0.05

Appendix 3c. Tukey's test. Cumulative linear growth *Porites cylindrica*.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	964.75	321.58	9.26*	4.32
B(A): Clone	11	107.17	8.93		
Error	22	578.83	177.08		
Total	35	1650.75			

* Term significant at alpha = 0.05

Appendix 3d. Tukey's test. Linear growth rate for *Porites cylindrica*.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	6.21	2.07	6.58*	4.32
B(A): Clone	11	1.89	0.16		
Error	22	4.07	0.97		
Total	35	12.17			

* Term significant at alpha = 0.05

Appendix 3e. Tukey's test. Basal width growth for *Acropora pulchra*.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	232.89	77.63	0.38	4.32
B(A): Clone	11	8.22	0.69		
Error	22	195.78	3.45		
Total	35	436.89			

* Term significant at alpha = 0.05

Appendix 3f. Tukey's test. Cumulative basal width growth rate for *Acropora pulchra.*

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	0.44	0.15	2.72	4.32
B(A): Clone	11	1.17	0.1		
Error	22	1.12	0.13		
Total	35	2.73			

* Term significant at alpha = 0.05

Appendix 3g. Tukey's test. Cumulative basal width growth for *Porites cylindrica*.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	53.64	17.88	1.66	4.32
B(A): Clone	11	6.06	0.5		
Error	22	79.28	5.79		
Total	35	138.97			

* Term significant at alpha = 0.05

Appendix 3h. Tukey's test. Basal width growth rate for *Porites cylindrica*.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	0.14	0.05	0.8	4.32
B(A): Clone	11	0	0		
Error	22	0.33	0.01		
Total	35	0.48	0.32		

* Term significant at alpha = 0.05

Appendix 3i. Tukey's test. Branch number for *Acropora pulchra*.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	29.06	9.69	2.14	4.32
B(A): Clone	11	7.87	0.66		
Error	22	19.09	1.76		
Total	35	56.02			

* Term significant at alpha = 0.05

Appendix 3j. Tukey's test. Branch number for *Porites cylindrica*.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	13.74	4.58	1.29	4.32
B(A): Clone	11	6.23	0.52		
Error	22	13.91	0.8		
Total	35	33.88			

* Term significant at alpha = 0.05

Appendix 3k. Tukey's test. Branch orientation for *Porites cylindrica*.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	172.48	57.49	12.72*	4.32
B(A): Clone	11	37.18	3.1		
Error	22	332.57	125.47		
Total	35	542.23			

* Term significant at alpha = 0.05

Appendix 3l. Tukey;s test. Total growth (weight) for *Acropora pulchra*.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	216.16	73.05	6.05*	4.32
B(A): Clone	11	85.84	7.15		
Error	22	327.64	73.3		
Total	35	632.64			

* Term significant at alpha = 0.05

Appendix 3m. Tukey's test. Totla growth (weight) for *Porites cylindrica*.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Critical Value (F) (α = 0.05, 1,21)
A: Treatment	2	550.08	183.36	9.64	4.32
B(A): Clone	11	204.64	17.05		
Error	22	346.63	109.04		
Total	35	1101.35			

* Term significant at alpha = 0.05

Appendix 4. ANOVA tables:

Appendix 4a. Analysis of Variance (ANOVA). Cumulative linear growth for *Acropora pulchra*. Table corresponds with Figure 5, page 19

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	2733.246	1366.623	3.51	0.041407*	0.614421
B(A): Clone	33	12840.02	389.0916			
C: Month	6	22864.13	3810.689	150.47	0.000000*	1.000000
AC	12	1130.698	94.22487	3.72	0.000044*	0.998314
BC(A)	198	5014.31	25.32479			
S	0					
Total (Adjusted)	251	44582.41				
Total	252					

* Term significant at alpha = 0.05

Appendix 4b. ANOVA. Linear growth rate for *Acropora pulchra*. Table corresponds with Figure 7, page 21

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	20.15336	10.07668	8.64	0.000960*	0.953717
B(A): Clone	33	38.48438	1.166193			
C: Month	5	52.19676	10.43935	15.89	0.000000*	1.000000
AC	10	29.42303	2.942303	4.48	0.000014*	0.998979
BC(A)	165	108.4219	0.6571023			
S	0					
Total (Adjusted)	215	248.6794				
Total	216					

* Term significant at alpha = 0.05

Appendix 4c. ANOVA. Cumulative linear growth for *Porites cylindrica*. Table corresponds with Figure 9, page 22

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	1.256069E-02	6.280346E-03	1.05	0.362101	0.217396
B(A): Clone	33	0.1978052	5.994097E-03			
C: Month	6	0.5521293	9.202155E-02	138.64	0.000000*	1.000000
AC	12	7.903087E-03	6.585906E-04	0.99	0.457686	0.568645
BC(A)	198	0.1314217	6.637461E-04			
S	0					
Total (Adjusted)	251	0.90182				
Total	252					

* Term significant at alpha = 0.05

Appendix 4d. ANOVA. Linear growth rate for *Porites cylindrica.* Table corresponds with Figure 10, page 23

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	1.286458	0.6432292	1.50	0.237651	0.296836
B(A): Clone	33	14.13802	0.4284249			
C: Month	5	3.783854	0.7567708	2.66	0.024320*	0.801080
AC	10	3.765625	0.3765625	1.32	0.221901	0.663242
BC(A)	165	46.96094	0.2846117			
S	0					
Total (Adjusted)	215	69.9349				
Total	216					

* Term significant at alpha = 0.05

Appendix 4e. ANOVA. Cumulative basal width growth for *Acropora pulchra*. Table corresponds with Figure 13, page 25

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	56.88889	28.44444	1.34	0.276129	0.268228
B(A): Clone	33	701.3333	21.25253			
C: Month	6	2247.54	374.5899	178.72	0.000000*	1.000000
AC	12	28.88889	2.407408	1.15	0.323131	0.648745
BC(A)	198	415	2.09596			
S	0					
Total (Adjusted)	251	3449.651				
Total	252					

* Term significant at alpha = 0.05

Appendix 4f. ANOVA. Basal width growth rate for *Acropora pulchra*. Table corresponds with Figure 15, page 26

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	3.009259E-02	0.0150463	0.11	0.892657	0.065996
B(A): Clone	33	4.357639	0.1320497			
C: Month	5	2.971065	0.5942129	8.09	0.000001*	0.999613
AC	10	0.8240741	8.240741E-02	1.12	0.348809	0.574040
BC(A)	165	12.12153	7.346381E-02			
S	0					
Total (Adjusted)	215	20.3044				
Total	216					

* Term significant at alpha = 0.05

Appendix 4g. ANOVA. Cumulative basal width growth for *Porites cylindrica*. Table corresponds with Figure 14, page 25

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	6.579365	3.289683	0.46	0.635200	0.118688
B(A): Clone	33	235.9405	7.149712			
C: Month	6	1481.873	246.9788	255.17	0.000000*	1.000000
AC	12	14.19841	1.183201	1.22	0.269652	0.683296
BC(A)	198	191.6429	0.9678932			
S	0					
Total (Adjusted)	251	1930.234				
Total	252					

* Term significant at alpha = 0.05

Appendix 4h. ANOVA. Basal width growth rate for *Porites cylindrica*. Table corresponds with Figure 16, page 26

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	2.141204E-02	1.070602E-02	0.26	0.771297	0.087808
B(A): Clone	33	1.349826	4.090383E-02			
C: Month	5	5.657697	1.131539	19.44	0.000000*	1.000000
AC	10	1.374421	0.1374421	2.36	0.012338*	0.927429
BC(A)	165	9.603298	5.820181E-02			
S	0					
Total (Adjusted)	215	18.00665				
Total	216					

* Term significant at alpha = 0.05

Appendix 4I. ANOVA. Branch number for *Acropora pulchra*. Table corresponds with Figure 17, page 27

Analysis of 4ariance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	7.869431	3.934716	2.70	0.082276*	0.497123
B(A): Clone	33	48.15117	1.459126			
S	0					
Total (Adjusted)	35	56.0206				
Total	36					

* Term significant at alpha = 0.05

Appendix 4J. ANOVA. Branch number for Porites cylindrica. Table corresponds with Figure 18, page 28

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	6.228021	3.114011	3.72	0.035016*	0.640680
B(A): Clone	33	27.64891	0.8378458			
S	0					
Total (Adjusted)	35	33.87693				
Total	36					

* Term significant at alpha = 0.05

Appendix 4K. Table of values for *Rayleigh's test for Circular Uniformity;* by treatment. Count data was transformed into Sine and Cosine values for the test. The 'z' value is compared to a table of critical values from which the hypothesis is either rejected or accepted. For this test, the null hypothesis was: Branches were distributed uniformly around the circle; with the fragment, viewed from above, being in the center of the circle.

	Clones											
Apart	1	2	3	4	5	6	7	8	9	10	11	12
n	19	14	14	7	8	14	9	15	16	18	19	11
r	0.1093	0.8162	0.2637	0.6142	0.8246	0.3333	0.8201	0.4249	0.5539	1.0708	0.2099	1.0544
R	2.0784	11.427	3.6918	4.299	6.5968	4.666	7.3815	6.3738	8.8624	19.275	3.9886	11.599
z	0.24	7.2541	0.7572	1.0272	2.4177	1.2099	3.0271	2.257	4.3635	20.642	0.8838	7.4745
Z (0.05, *n*)	2.956	2.941	2.941	2.885	2.899	2.941	2.91	2.945	2.948	2.945	2.956	DNR
Decision	DNR	Reject	DNR	DNR	DNR	DNR	Reject	DNR	Reject	Reject	2.926	Reject

	Clones											
Near	1	2	3	4	5	6	7	8	9	10	11	12
n	16	6	N/A	N/A	14	19	N/A	18	14	18	11	11
r	0.4113	0.8345			0.0691	0.4426		0.3285	0.5728	0.0304	0.8928	0.6971
R	6.5811	5.0071			0.9684	8.4103		5.9134	8.0193	0.5476	9.8212	7.6687
z	2.4062	1.3929			0.0521	3.9297		1.9427	3.5728	0.0167	5.3587	3.2672
Z (0.05, *n*)	2.948	2.865			2.941	2.956		2.954	2.941	2.954	2.926	2.926
Decision	DNR	DNR			DNR	Reject		DNR	Reject	DNR	Reject	Reject

	Clones											
Crowded	1	2	3	4	5	6	7	8	9	10	11	12
n	10	N/A	10	7	6	11	13	N/A	13	16	7	N/A
r	0.2686		0.6728	0.9669	1.3194	1.2484	0.5948		0.6856	0.6552	0.1954	
R	2.6862		6.7284	6.7686	7.9165	13.7328	7.7323		8.9132	10.4827	1.3681	
z	0.4009		2.5151	2.5452	3.4817	10.477	3.3216		4.4136	6.1049	0.104	
Z (0.05, *n*)	2.919		2.919	2.885	2.865	2.926	2.937		2.937	2.948	2.885	
Decision	DNR		DNR	DNR	Reject	Reject	Reject		Reject	Reject	DNR	

Appendix 4L. ANOVA. Branch orientation for *Porites cylindrica*. Values used for this test were the 'z' values obtained from the *Rayleigh's Test for Circular Uniformity.*

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	37.17931	18.58965	1.21	0.309741	0.246522
B(A): Clone	33	505.0511	15.30458			
S	0					
Total (Adjusted)	35	542.2303				
Total	36					

* Term significant at alpha = 0.05

Appendix 4M. ANOVA. Total growth (weight) for Acropora pulchra. Table corresponds with Figure 19, page 30

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	153.6981	76.84904	5.03	0.012416*	0.778884
S	33	504.3948	15.28469			
Total (Adjusted)	35	658.0928				
Total	36					

* Term significant at alpha = 0.05

Appendix 4N. ANOVA. Total growth (weight) for *Porites cylindrica*. Table corresponds with Figure 20, page 30

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Treatment	2	204.6394	102.3197	3.77	0.033651*	0.646758
S	33	896.7135	27.17314			
Total (Adjusted)	35	1101.353				
Total	36					

* Term significant at alpha = 0.05

Appendix 4M. ANOVA. Flow rates for manifolds between each water table.

Analysis of Variance Table

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (α = 0.05)
A: Table	1	0.10125	0.10125	0.36	0.554762	0.089365
B: Nozzle	35	19.87153	0.567758			
AB	35	9.96375	0.2846786			
S	0	0				
Total (Adjusted)	71	29.93653				
Total	72					

* Term significant at alpha = 0.05