Alkalinity enhancement for improved grow-out in ex-situ tanks of priority coral species for restoration

Images of the five coral species used in the study (*Pseudodiploria strigosa*, *Diploria labyrinthiformis*, *Colpophyllia natans*, *Montastrea cavernosa*, *Orbicella faveolata*).

Alkalinity enhancement for improved grow out in ex-situ tanks of priority coral species for restoration

Final Report

Prepared By:

Chris Langdon

University of Miami

May/2026

Completed in Fulfillment of C5B4A2 for

Florida Department of Environmental Protection
Coral Protection and Restoration Program
8000 N Ocean Dr.
Dania Beach, FL 33004

This report should be cited as follows:
Langdon, Chris. 2026. Alkalinity enhancement for improved grow out in ex-situ tanks of priority coral species for restoration**. Florida DEP Coral Protection and Restoration Program. Miami, FL. Pp. 1-26.**

This report was funded through a contract agreement from the Florida Department of Environmental Protection's (DEP) Coral Protection and Restoration Program. The views, statements, findings, conclusions, and recommendations expressed herein are those of the author(s) and do not necessarily reflect the views of the State of Florida or any of its subagencies.

Acknowledgements

Nicole Fogarty at UNCW is gratefully acknowledged for supplying the *Pseudodiplora strigosa*, *Montastraea cavernosa* and *Orbicella faveolata* junvenile corals used in this study. Keri O'Neil and Brian Reckenbeil at The Florida Aquarium are gratefully thanked for supplying the *Colpophyllia natans* and *Diploria labyrinthiformis* juvenile corals used in the study. Cam McMath at the UM Reef Futures facility, is gratefully acknowledged for sharing his facility for the conduct of this experiment.

Management Summary (300 words or less)

The goal of this project was to determine the degree to which the growth rate of massive coral species, identified as a priority for coral restoration projects, can be increased by adding alkaline chemicals (sodium carbonate and bicarbonate) to the water in which they are raised. The study was conducted over a six-month period. The five species tested were *Colpophyllia natans* (CNAT), *Siderastrea siderea* (SSID), *Orbicella faveolata* (OFAV), *Montastraea cavernosa* (MCAV) and *Pseudodiploria strigosa* (PSTR). The study found that growth rates can be increased by 1.8 to 1.9-fold. The management significance is that it may be possible to raise sexually propagated corals to outplantable size in less time, thereby allowing land-based nurseries to produce more corals for restoration projects.

Priority addressed: This project responds to CRP FY25-26 research priority ER2. Specifically, it aims to identify a practical way to improve the efficiency and output of ex situ nurseries that produce priority coral species for restoration projects. "ER2. Further development of techniques, strategies, and interventions to enhance reproduction, settlement, growth, and survival in in situ and ex situ coral sexual propagation efforts. Research should focus on the development, refinement, and testing of innovative techniques and technologies to improve propagation success, efficiency, and output. Priority species for 2025 are ACER (in Southeast Florida), APAL (in the Florida Keys), CNAT, DLAB, MCAV, OFAV, and PSTR; other species will be considered with justification."

Reef management application: Using information from this project, land-based nursery operators anywhere in Florida can follow easy-to-follow instructions to dose their tanks with sodium carbonate and bicarbonate to significantly increase the production rate of high-priority brain/boulder corals for restoration projects.

Executive Summary (max 1 page)

Coral restoration projects are increasingly relying on the use of sexually propagated corals. This is driven by the need to restore not just the number of coral outplants on Florida's depopulated reefs, but also their genetic diversity. Sexually propagated corals start out life extremely small and cannot be outplanted immediately because mortality due to predation is extremely high. As a result, sexually propagated corals are generally raised in land-based nurseries until they are of outplantable size. Managers also want to restore heat-tolerant corals. Experience from the 2023 marine heatwave was that many species of brain and boulder corals, while severely bleaching, generally showed good recovery. As a result, DEP's Coral Protection and Restoration (CRP) has identified five brain and boulder corals as being priority species for sexual propagation and restoration. Unfortunately, these species grow very slowly, and it typically takes 2-3 years to raise them to a safe, outplantable size. This slow growth creates a bottleneck in annual coral production. This project asked the research question, "Can the grow-out time be significantly reduced by optimizing the carbonate chemistry of the seawater for the maximum rate of skeletal growth?" The results of the 2025 experiments are promising. Skeletal growth based on an increase in buoyant weight over six months increased 1.8 to 2.3-fold in the five species tested. This means that it may be possible to significantly reduce the grow-out for these species. Using information from this project, dosages for sodium carbonate and bicarbonate can be shared with land-based nursery operators anywhere in Florida to significantly increase the production rate of high-priority brain/boulder corals for restoration projects.

Table of Contents

1. INTRODUCTION

In order for coral reef restoration projects using more heat stress-tolerant but slower growing coral species (CNAT, SSID, OFAV, MCAV, PSTR) to become scalable, it will be necessary to create a production pipeline where these corals are produced by sexual propagation and then raised to a viable outplanting size in land-based nursery facilities at many locations around the state. The efficiency of the pipeline producing outplantable-size corals from the land-based nurseries will benefit from optimization of the growth

conditions in the tanks. Feeding corals the recommended amounts and optimizing lighting are obvious steps that every aquarist can take. Another step is to optimize the water's chemical condition. Corals use Ca^{2+} and CO_3^{2-} ions found in seawater as the building blocks for their calcium carbonate skeletons. The rate at which these ions combine to form crystals of $CaCO_3$ is dependent on their concentration. The higher the concentration of either ion, the faster the crystals are formed and the faster the coral can build its skeleton. The concentration of Ca^{2+} in seawater is quite high (10 mM) while the concentration of CO_3^{2-} is typically 200 uM. As a result, the availability of CO_3^{2-} is generally considered to be 'rate limiting'. Corals are living organisms, and many other factors also impact the rate of skeleton building, including temperature, light, and food availability. However, when these other factors are optimized, such as in a land-based nursery, the availability of CO_3^{2-} can become the rate-limiting factor. This, in turn, means that if the CO_3^{2-} concentration is increased, the rate of skeletal formation can increase. However, it will only be possible to increase the rate of skeleton building by a certain amount before a biological factor becomes rate-limiting. The study reported here aimed to determine the extent to which the growth of five coral species can be increased by adding sodium carbonate and bicarbonate salts to seawater.

During the early days of ocean acidification research, investigators conducted experiments at low, normal, and high carbonate concentrations to simulate conditions in the future, present day, and past. Those studies found that coral calcification rates could be increased by 1.2 to 2.3-fold by increasing carbonate concentration (Table 1).

Source	Species	$[CO_3^{2-}]$, µmol/kg	Calcification, mg/cm^2/d	Increase, x fold
Marubini et al 2001	*Porites compressa*	183	1.48	1.2
		373	1.84	
Schneider and Erez 2006	*Acropora eurystoma*	180	0.26	2.0
		371	0.52	
Odhe and Hussain 2004	*Porties lutea*	288	0.045	2.3
		572	0.105	
Langdon et al 2000	*mixed community*	239	60	1.9
		375	114	
Marubini and Thake 1999	*Porites porites*	153	5.5	2.1
		442	11.3	

Table 1. Compilation of studies where carbonate concentration has been increased much beyond the present day.

In preparation for this project MS student Veronica Paul in the Langdon lab conducted an experiment at the Reef Futures University of Miami (UM) facility utilizing replicated 5-gallon aquarium tanks containing assemblages (n=6 pieces each) of SSID, MCAV, PSTR, OFAV, *Acropora cervicornis* (ACER), *Acropora palmata* (APAL), and *Acropora prolifera* (APRO). Sodium carbonate and bicarbonate were added in 2:1 ratio to increase carbonate concentration while minimally increasing pH. The results show that increasing carbonate concentration to 500 umol/kg, roughly doubles the calcification rate of the mixed coral species assemblages.

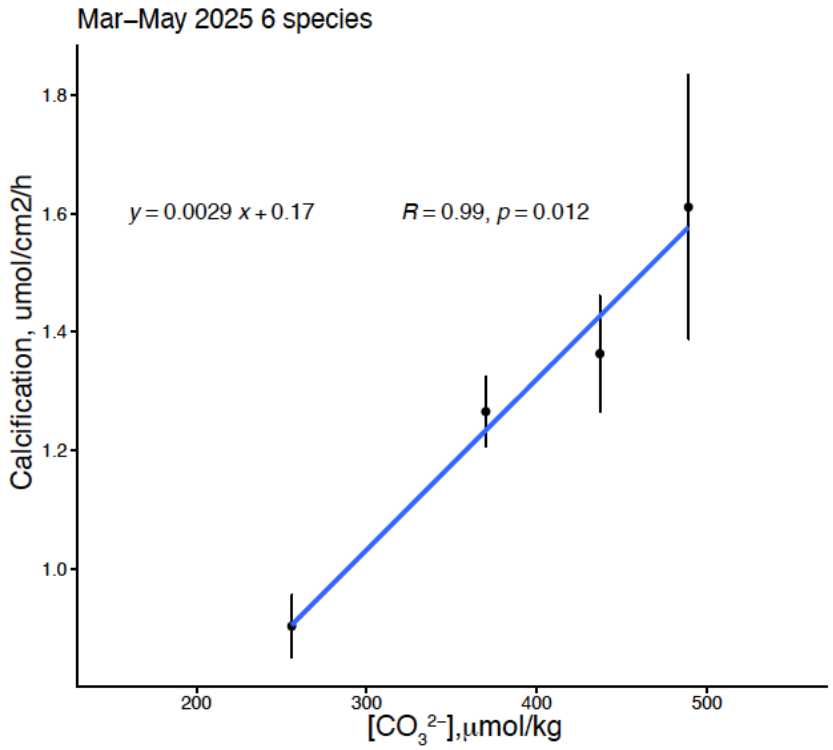

Figure 1. Calcification rate (micro-moles of CaCO3/cm2/h) of racks of mixed assemblages of corals exposed to six different levels of enhanced alkalinity (preliminary results).

Based on the literature review (Table 1) and the results of the initial trials in the Langdon Lab (Figure 1) it was decided that there was adequate justification to propose a

study to Florida DEP that would conduct a test of the concept on five coral species identified as being a priority for coral restoration.

Project Goals

Key goals and objectives

- Determine how much the growth of each test species can be increased through alkalinity enhancement.
- Determine the relative effectiveness of alkalinity enhancement for test species.
- Identify an optimum level of alkalinity enhancement beyond which growth saturates or starts to decrease for test species.
- Determine whether somatic tissue growth can keep pace with increased skeletal growth during alkalinity enhancement.

2. METHODS AND MATERIALS

2.1. Experimental Design

The experiment consisted of five groups of corals (n=25), each comprising five pieces of each of the five species. Corals for the five groups were chosen haphazardly from the 60 pieces we had of each species. Each group of corals was then placed in a 5-gallon glass aquarium tank filled to the marked level to assure a constant volume from day to day. Each morning the water in the aquaria was changed and the pre-measured amounts of sodium carbonate and bicarbonate salts were added to achieve the desired Ω_{arag}. At midday a water sample was drawn from each tank and analyzed for TA and pH to allow for confirmation of the desired treatment levels. The data were analyzed in two ways. First, a linear regression model was used to test for a significant correlation between the different dependent variables (calcification, planar growth, vertical growth) and the independent variables Ω_{arag} or carbonate ion concentration. Second, the treatments were grouped into a low group consisting of treatments 1 and 2) and a high group consisting of treatments 3, 4 and 5). This grouping permitted analysis of the data using a t-test.

2.2. Coral husbandry

2.2.1. Experimental setup

This experiment consisted of five aquaria placed inside three raceways at the University of Miami Experimental Hatchery. The aquaria were rotated through the raceways daily to ensure they received equal amounts of sunlight. They were emptied, refilled, and treated daily to maintain the desired concentration of carbonate ions. The water temperatures were controlled at 28°C, and the aquaria were filled with 28 liters of seawater.

Figure 1. The setup at the University of Miami Experimental Hatchery. Five aquaria inside three raceways.

Varying levels of sodium bicarbonate and carbonate were added to each aquarium to raise the aragonite saturation state (**Ω**Arag), resulting in five independent treatments, including a control that received no treatment. The amounts of sodium bicarbonate and carbonate added are shown in the table below.

Table 2. The target $\mathbf{\Omega}_{Arag}$ and the amounts of sodium bicarbonate and carbonate added to achieve the desired carbonate concentrations in each treatment.

Treatment	$\mathbf{\Omega}_{Arag}$	Sodium Bicarbonate (g)	Sodium Carbonate (g)
1 (control)	4.0	.000	.000
2	6.0	1.089	0.187
3	8.0	1.877	0.368
4	10.0	2.566	0.546
5	11.0	2.966	0.721

Twenty-five coral recruits were placed in each aquarium, five of each species (*C. natans, D. labyrinthiformis, P. strigosa, O. faveolata, M. cavernosa),* for a total of 125 corals in the experiment. The coral recruits were sourced from University of North Carolina Wilmington Coral REEF Lab and The Florida Aquarium.

2.2.2. Coral labeling

Corals were labeled with letter-number designations to identify them. Every coral of the same species had the same letter (*P. strigosa: A; M. cavernosa: B; O. faveolata: C; D. labyrinthiformis: D; C. natans: E),* then received a number from 1-25 to correspond to their treatments (1-5: Treatment 1; 6-10: Treatment 2; 11-15: Treatment 3; 16-20: Treatment 4; 21-25: Treatment 5).

2.2.3. Coral Feeding

Corals were fed twice a week with a solution of .25g of Aquatic Foods Golden Pearls (300-500 microns), .25g of Reef-Roids®, and .25g of Benepets™ Benereef™. The solution was mixed with 4 ounces of aquarium saltwater from a squeeze bottle. The

corals were target-fed by squeezing the bottle over each coral until a cloud of food surrounded it. The corals sat for 30 minutes to take in the food, then the water was changed, and 5 mL of Acropower Amino Acid Formula was added.

2.2.4. Cleaning

Coral plugs were cleaned once a week using brushes, tweezers, and snips to remove algae and encrusting organisms, thereby helping ensure accurate buoyant weights and preventing corals from becoming overgrown. The raceways and aquaria were drained, wiped down, and refilled once a week to mitigate algae growth.

2.3. Data collection and analysis

2.3.1. Buoyant weight

To determine coral skeletal growth rate, the buoyant weight of each coral was measured weekly (Jokiel, P. L., et al., 1978). The average difference between the weekly weights and the water's aragonite saturation state was used to calculate the corals' growth rate.

Figure 2. Buoyant weighing apparatus.

2.2.2 *Surface area*

Pictures of the corals were taken monthly to calculate the surface area to determine planar areal growth rate. Pictures were taken with an Andonstar Digital Microscope 246-249 series, using a 12-320mm lens. The corals were placed on an egg crate and stood vertically under the camera. The images were then uploaded into ImageJ to calculate the surface area of the corals.

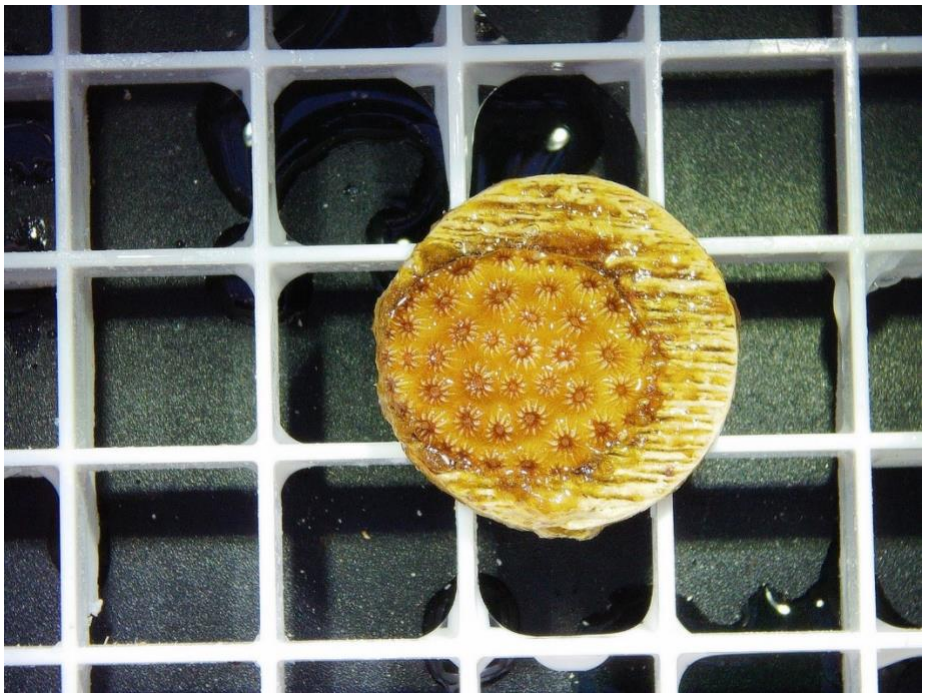

Figure 3 . O. faveolata on egg crate used for scaling image for surface area measurement.

2.3.2. Vertical extension

Measuring vertical extension growth in corals provided another way to assess their skeletal growth. The vertical extension growth was measured weekly using a Keyence Optical Micrometer Intelligent-G Laser Sensor.

Figure 4. Keyence Intelligent-G Laser Sensor Optical Micrometer used for measuring the vertical growth of the corals.

2.3.3. Water quality

Water samples were collected weekly and analyzed first with a spectrophotometer to measure the pH (total scale) of the water in each aquarium (Clayton and Byrne, 1993). Water samples were then filtered to remove any organic particles and bubbled with CO_2 gas for 20 seconds. Filtration and CO_2 bubbling are necessary to prevent CaCO3 precipitation in highly supersaturated samples (Schultz et al., 2023). Then the samples were analyzed for total alkalinity (TA) (Breeland and Byrne, 1993). Finally, the $\mathbf{\Omega}_{Arag}$ and carbonate ion concentrations were calculated from TA and pH using the seacarb package in R.

2.3.4. Pulse amplitude modulation (PAM)

The pulse amplitude modulation (PAM) fluorometry, introduced by Schreiber et al. (1986), measures the photosynthetic efficiency of the coral symbiotic algae. The PAM technique uses two light sources: one continuous light source and a short (1 second) saturating pulse to drive photosynthesis (Fm), and another, very short (1-5 µs) and

usually weak, to measure fluorescence without driving photosynthesis (Fv). Corals must be dark-adapted for 20 minutes before PAM is initiated. A Walz Diving-PAM-II Underwater Flourometer was used for PAM measurements. The ratio of variable fluorescence (Fv) to maximum fluorescence (Fm) indicates the photosynthetic efficiency of photosystem II in symbiotic algae and provides insight into whether symbionts are experiencing stress that could reduce the energy available to the coral polyp.

Figure 5. Tent used to provide a dark place for using PAM fluorometer to measure photosynthetic efficiency.

2.3.5. Respirometry

Respirometry measures the net amount of photosynthate produced by the symbionts in the light. Respirometry was done between 1000 and 1400 hours on a sunny day, when photosynthetic rates are expected to be light-saturated, using a PreSens Precision Oxy-4. Oxygen concentrations were measured every 5 seconds. The rates of net

photosynthesis were determined by regressing oxygen concentration against time. Rates were corrected for an empty chamber background rate of oxygen consumption.

Figure 6. The respirometry setup comprised a laptop computer, a Presens OXY4 oxygen analyzer (in a Pelican case), and glass jars in the raceway tank. Eight corals could be measured at one time. Readings were sent to the computer at 5-second intervals.

2.3.6. Statistical analyses

Linear regression analysis was performed to test for a statistically significant relationship between carbonate ion concentration and calcification rate for each species. T-tests were performed to assess statistically significant relationships among calcification, planar area growth, vertical extension, photosynthetic efficiency, and net photosynthesis for each species. For these tests, the results for treatments 1 and 2 were pooled and called the 'lo' carbonate group, and treatments 3, 4, and 5 were pooled and called the 'hi' carbonate group. The grouping was done to ensure the data met the assumptions of parametric tests. Statistical analyses and graphical plots will be performed using RStudio 2026.04.0.

3. RESULTS

3.1. Calcification rates

Figure 1 shows the mean calcification rates for all treatments, with standard error bars, along with a linear regression line. It shows that every treatment increased the calcification rate in each species compared to the control group. DLAB showed a weak linear correlation (R2 = 0.34), while the other 4 species showed moderate to strong linear correlations in calcification rates across treatments.

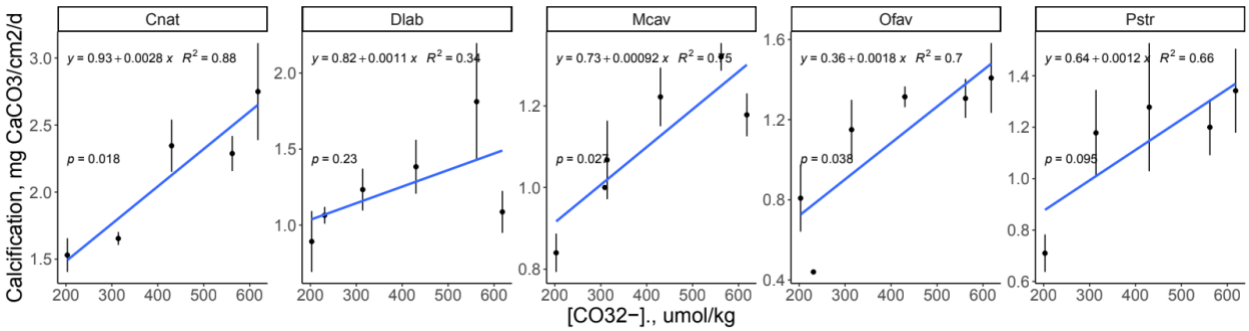

Figure 1. The calcification rates (mean ± standard error) for all species in all treatments through the experiment. The carbonate ion concentration (CO_3^{-2}) in ***μ****mol/kg identifies that the control has an average of 228 ± 3.72, and treatment 5 has an average of 589 ± 8.56. Linear regression was used to test significant differences in calcification for the treatments. An R^2 value closer to 1 or -1 indicates a linear correlation between the treatments.*

Treatments were grouped into low (lo) and high (hi) levels for data analysis, allowing a t-test to test for a significant difference. The low treatment group consisted of the control and treatment 2. The high treatment group consisted of treatments 3, 4, and 5. Figure 2 shows that, even after grouping treatments, calcification rates remain significantly higher in the high treatments than in the low treatments for each species. The increase in the growth rate appears less drastic because treatments 3, 4, and 5 were grouped into a single category.

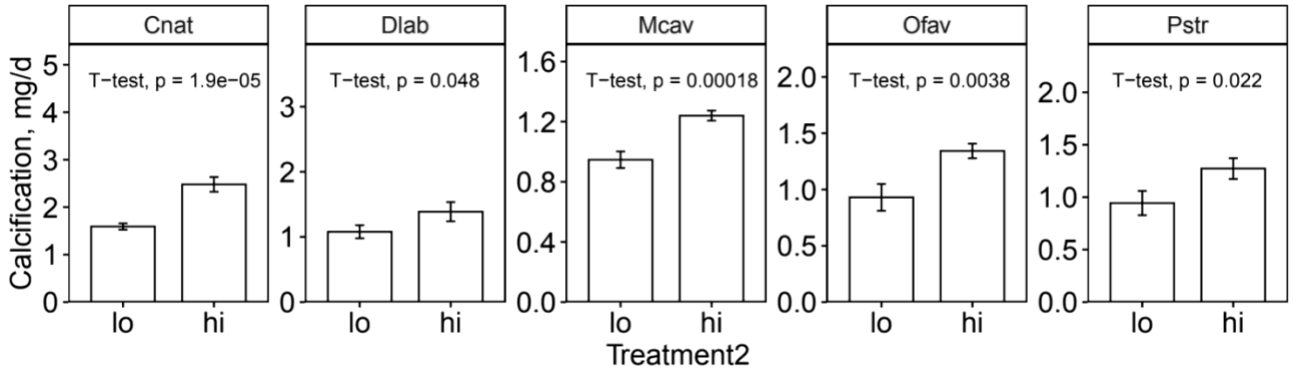

Figure 2. The calcification rates (mean ± standard error) for the low- and high-treatment groups. A T-test was conducted to assess significant differences between groups. The p-values indicate a significant increase in the calcification rates for all species between the low and high treatments.

3.2. Surface area

Figure 3 shows the mean surface area growth for the low and high treatments. All species showed increased surface area growth, but only MCAV and OFAV showed a significant increase in surface area (lateral growth) between the low and high treatments, while the brain coral species showed an increase that was not significantly different.

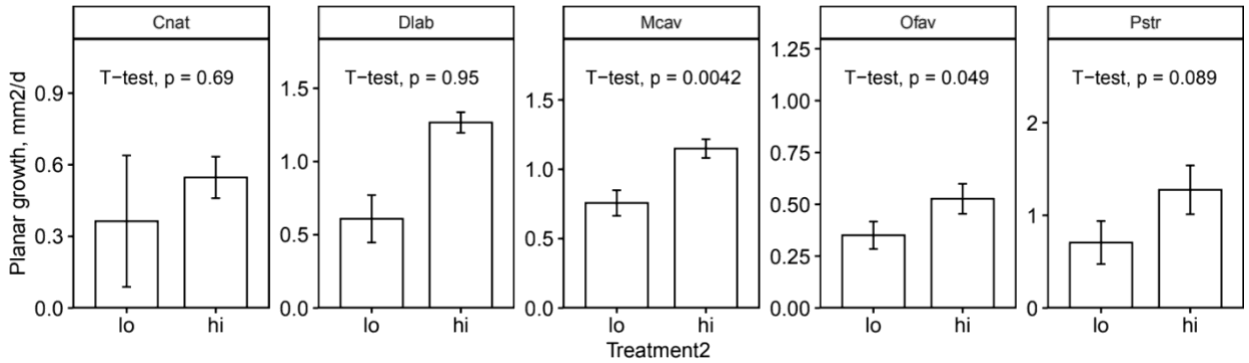

Figure 3. The surface area, or lateral growth, (mean ± standard error) for the low and high treatment groups. A T-test was conducted to assess significant differences between groups. The p-values indicate a significant increase in the star coral (MCAV and OFAV) surface area growth, but no statistical difference for the brain coral species (CNAT, DLAB, and PSTR).

3.3. Vertical extension

Figure 4 shows the mean vertical growth for low and high treatments. None of the species is statistically different in vertical growth between the low and high treatments. This is expected because these are bouldering corals thatdon’t usually grow vertically,

unlike branching corals like Acropora, which could explain why there isn't a difference in vertical extension growth.

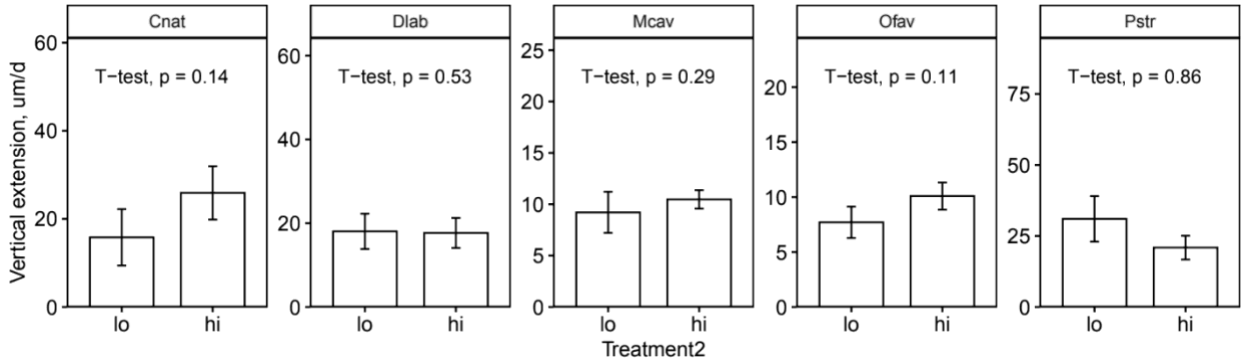

Figure 4. Vertical growth (mean ± standard error) for the low- and high-treatment groups. A T-test was conducted to assess significant differences between groups. The p-values indicate no statistically significant difference in vertical growth between the low and high treatments across species.

3.4. PAM

Figure 5 indicates the median photosynthetic efficiency by the dark bar, while the whiskers represent standard error. With the other three species, PSTR, OFAV, and MCAV, the high treatments showed a significant decrease in photosynthetic efficiency. However, all values above 0.5 are considered healthy and don’t indicate the stress levels you would expect during a high heat/bleaching event.

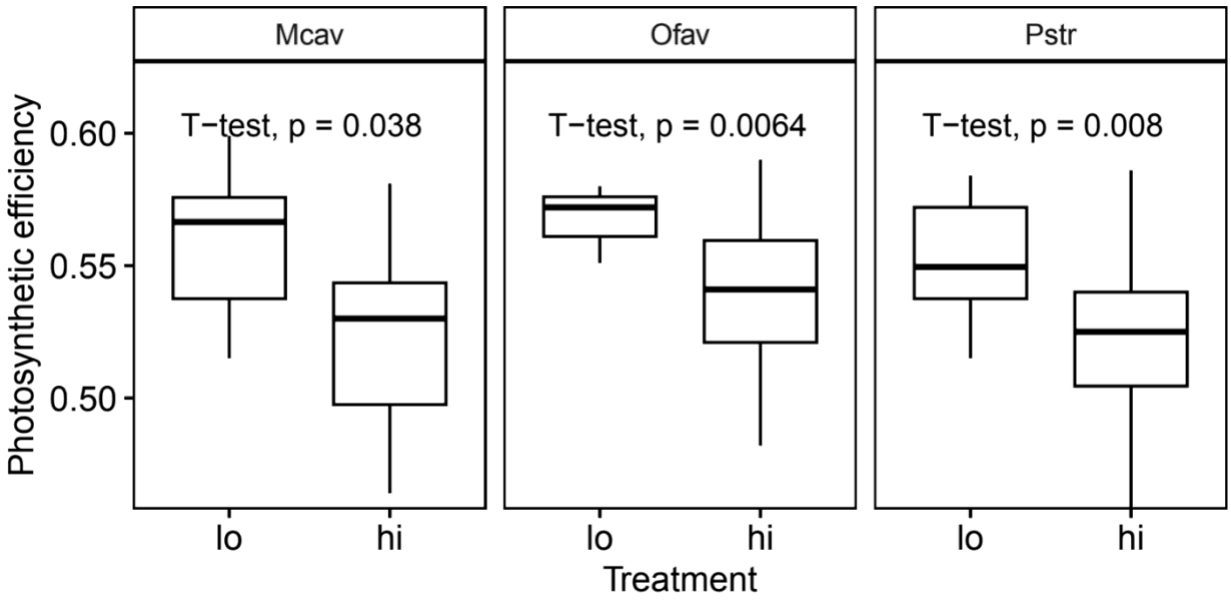

Figure 5. Photosynthetic efficiency rates (median ± standard error) for MCAV, OFAV, and PSTR for low and high treatment groups. DLAB and CNAT are excluded due to high mortality rates and insufficient replicates, rendering the data inaccurate. A photosynthetic efficiency rate above 0.5 is considered healthy for coral. A T-test was conducted to assess significant differences between groups. The p-values indicate a significant decrease in photosynthetic efficiency across all species.

3.5. Respirometry

Figure 6 shows the mean net photosynthesis for low and high treatments. For respirometry, only OFAV shows a significant increase in net photosynthesis between the low and high treatments, whereas MCAV and PSTR show no statistically significant difference between treatments.

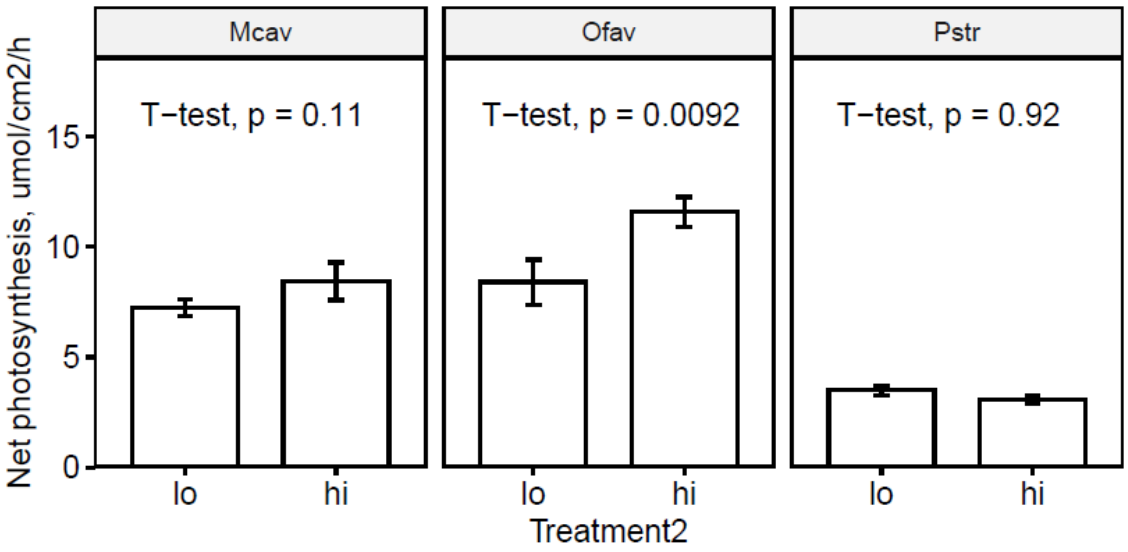

Figure 6. Net photosynthesis rate (mean ± standard error) for MCAV, OFAV, and PSTR for low and high treatment groups. A T-test was conducted to assess significant differences between groups. The p-values indicate that only OFAV had a significant increase in net photosynthesis.

3.6. Survivorship

Coral mortality was observed throughout the experiment. Figure 7 shows the number of replicate coral recruits for each species in each treatment. DLABs were the first to experience mortality, while the other species did not experience any mortality until a disease event that occurred mid-December.

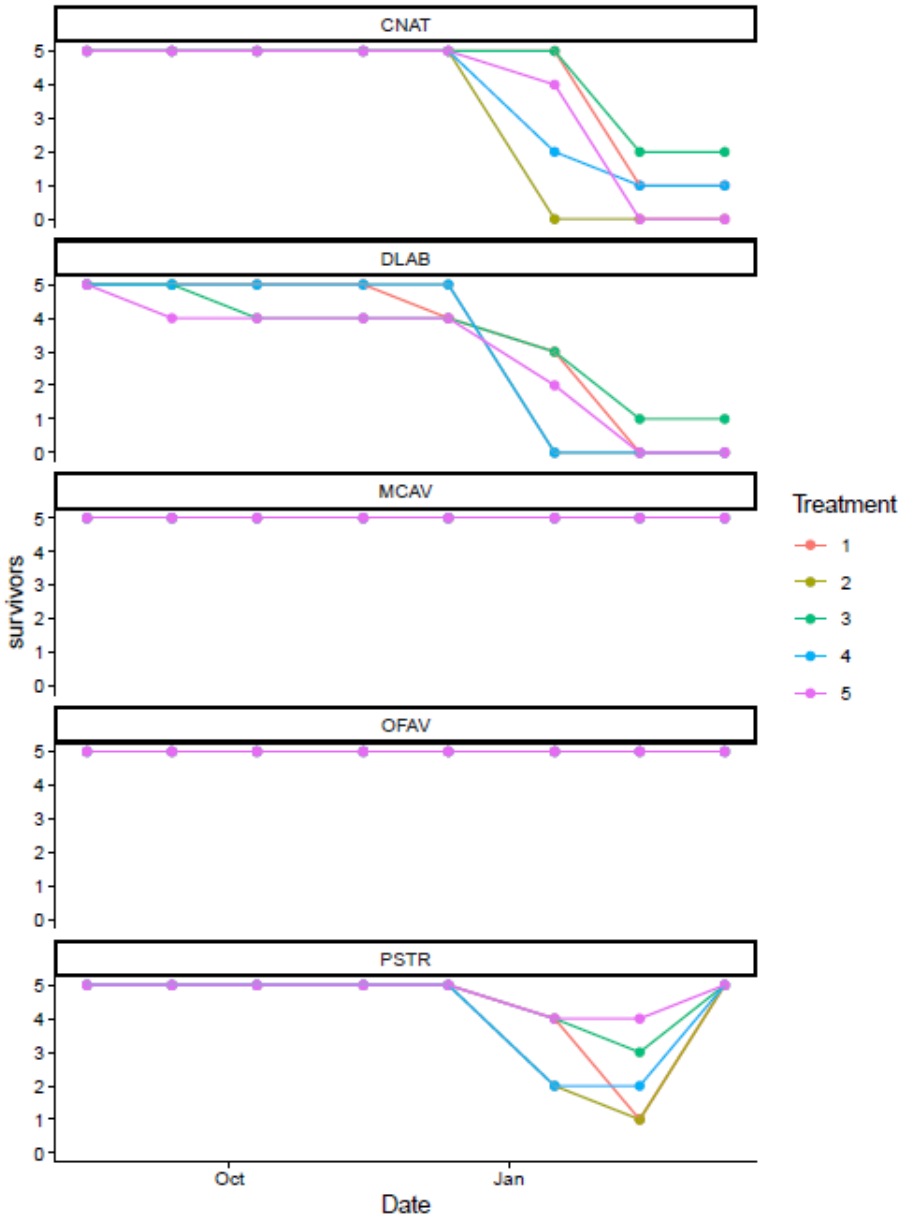

Figure 7. The number of surviving coral recruits replicates in each treatment throughout the experiment. Brain coral species were heavily affected by a disease in mid-December, which led to a decrease in their replicates. Mortality was not treatment-related, as all treatments, including the control, experienced mortality.

4. DISCUSSION

The calcification rate of all five massive coral species increased ~2-fold when comparing the control to treatment 5, indicating that these coral species calcify twice as quickly at the higher treatment levels. Although every coral species showed increased surface area growth, the difference was significant only for OFAV and MCAV, not for PSTR, DLAB, or CNAT. This could mean that calcification was more directed toward skeleton formation in brain coral species than toward lateral growth, resulting in denser skeletons than in the low-treatment groups. The PAM and respirometry results indicate that the symbionts were not adversely affected by the high alkalinity treatments. This means that concerns about somatic growth not keeping up with skeletal growth were unfounded. The optimal level of alkalinity varied by species. For CNAT, OFAV and PSTR the optimal carbonate concentration was 650 umol/kg. For DLAB and MCAV the optimal concentration was 550 umol/kg. The mortality of the brain coral species could also have affected the data, leading to no significant increase in surface area growth by reducing the number of replicates in some treatments. There was no significant difference in vertical growth among these 5 species. Since these are bouldering corals, we wouldn't expect the vertical growth to change much because they usually grow more laterally than they do vertically anyway.

The PAM and respirometry tests were run to provide insight into the photosynthetic abilities of the corals and how they were affected in the higher treatments. The results from PAM showed that during higher dosage treatments, OFAV, MCAV, and PSTR showed a significant decrease in their photosynthetic efficiency. A photosynthetic efficiency of 0.5 or higher indicates a healthy photosynthesizing coral; even though there was a significant decrease, it was not enough to consider the coral unhealthy, which would have a photosynthetic efficiency closer to 0.3. The respirometry results showed that OFAV exhibited a significant increase in net photosynthesis, indicating that organic tissue production was enhanced as well as skeletal growth. This is clearly good for the coral but the mechanism is not clear. MCAV showed a slight, non-significant increase in net photosynthesis, whereas PSTR showed a slight, non-significant decrease.

Throughout this experiment, some of these corals experienced mortality. It occurred randomly across treatments, including the control group, suggesting it was not

treatment-related. During December, a disease did come through, which mostly affected the brain coral species, while MCAV and OFAV came out rather unscathed. Affected corals across all treatments and the control began to suffer rapid tissue loss, and once again, this was mostly brain coral species. This disease outbreak could have affected the calcification rate of the other surviving corals and may also have affected the data by reducing the number of replicates in the experiment.

5. MANAGEMENT RECOMMENDATIONS

The study determined that elevated alkalinity dosages resulting in carbonate ion concentrations of 500-650 umol/kg can increase the growth of the studied species by twofold. Based on this finding, it is recommended that land-based nurseries use these dosages in the propagation pipeline to increase coral growth rates and shorten grow-out times. All coral species will likely benefit from alkalinity enhancement, but the biggest pay-off is likely to be for slowly growing massive species. Daily dosing, as employed in this study, is probably too labor-intensive for big land-based nurseries. However, the dosages can be adjusted for weekly dosing with some possible loss of benefit to growth.

It is recommended that research be conducted to answer four key questions.

1. Longer experiments (0.5 – 1 year) are needed to demonstrate that areal growth is enhanced to the same extent as skeletal mass increase.
2. Can carbonate ion concentrations of 500-600 umol/kg be achieved in the large raceway tanks typically used at land-based nursery operations? Can it be done with acceptable materials and labor costs?
3. Will corals that have been grown at high carbonate concentration experience detrimental effects when returned to ambient seawater carbonate concentration?
4. What happens to skeletal density when corals are raised at high carbonate concentration? Will density increase, and will that make them less prone to

predation by coralivorous fish, or will the density be reduced, resulting in greater loss to predation?

6. REFERENCES

Albright, R., Caldeira, K., Hosfelt, J., Kwiatkowski, L., Maclaren, J. K., Mason, B. M., ... & Andersson, A. J. (2016). Reversal of ocean acidification enhances net coral reef calcification. Nature, 531(7593), 362–365. https://doi.org/10.1038/nature17155

Allemand, D., Tambutté, É., Zoccola, D., Tambutté, S. (2011). Coral Calcification, Cells to Reefs. In: Dubinsky, Z., Stambler, N. (eds) Coral Reefs: An Ecosystem in Transition. Springer, Dordrecht. https://doi.org/10.1007/978-94-007-0114-4_9

Andersson, A. J., & Gledhill, D. (2013). Ocean acidification and coral reefs: Effects on breakdown, dissolution, and net ecosystem calcification. Annual Review of Marine Science, 5, 321–348. https://doi.org/10.1146/annurev-marine-121211-172241

Bednaršek, N., van de Mortel, H., Pelletier, G., García-Reyes, M., Feely, R., & Dickson, A. (2025). Assessment framework to predict sensitivity of marine calcifiers to ocean alkalinity enhancement – identification of biological thresholds and importance of precautionary principle. Frontiers in Marine Science, Biogeosciences, 22, 473-498. https://doi.org/10.5194/bg-22-473-2025

Comeau, S., Cornwall, C. E., & McCulloch, M. T. (2017). Decoupling between the response of coral calcifying fluid pH and calcification to ocean acidification. Nature Climate Change, 7(12), 1182–1188. https://doi.org/10.1038/s41558-017-0039-4

Cornwall, C. E., & Hurd, C. L. (2015). Experimental design in ocean acidification research: Problems and solutions. ICES Journal of Marine Science. https://doi.org/10.1093/icesjms/fsv118

Doney, S. C., Fabry, V. J., Feely, R. A., & Kleypas, J. A. (2009). Ocean acidification: The other CO2 problem. Annual Review of Marine Science, 1, 169–192. https://doi.org/10.1146/annurev.marine.010908.163834

Gattuso, J.-P., Allemand, D., & Frankignoulle, M. (1998). Effect of calcium carbonate saturation of seawater on coral calcification. Global and Planetary Change, 18, 37–46. https://doi.org/10.1016/S0921-8181(98)00035-6

Langdon, C., Broecker, W. S., Hammond, D. E., Glenn, E., Fitzsimmons, K., Nelson, S. G., ... & Atkinson, M. J. (2000). Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. Global Biogeochemical Cycles, 14(2), 639–654. https://doi.org/10.1029/1999GB001195

Manzello, D., Cunning, R., Karp, R., Baker, A., Bartels, E., Bonhang, R., Borreil, A., Borque, A., Brown, K., Bruckner, A., Corbett, B., D'Alessandro, M., Dahlgreen, C., Dilworth, J., Geiger, E., Gilliam, D., Gomez, M., Hanson, G., Harrell, C., …, Williamson, O. (2025). Heat-driven functional extinction of Caribbean *Acropora* corals from Florida's Coral Reef. *Science* **390**, 361-366. DOI:10.1126/science.adx7825

Mote Marine Laboratory Bleachwatch. (2005-2022). Coral Bleaching Early Warning Network Current Conditions Reports. Available online at: **https://mote.org/support/volunteer/citizen-science/bleachwatch/**

Neely K.L., Nowicki R.J., Dobler M.A., Chaparro A.A., Miller S.M., and Toth K.A. (2024). Too hot to handle? The impact of the 2023 marine heatwave on the Florida Keys coral. Front. Mar. Sci. 11:1489273. doi: 10.3389/fmars.2024.1489273

Opdyke, B. N., & Wilkinson, B. H. (1993). Carbonate mineral saturation state and cratonic limestone accumulation. American Journal of Science, 293, 217–234. https://doi.org/10.2475/ajs.293.3.217

Palacio-Castro, A. M., Enochs, I. C., Besemer, N., Boyd, A., Jankulak, M., Kolodziej, G., Hirsh, H. K., Webb, A. E., Towle, E. K., Kelble, C., Smith, I., & Manzello, D. P. (2023). *Coral reef carbonate chemistry reveals interannual, seasonal, and spatial impacts on ocean acidification off Florida*. *Global Biogeochemical Cycles, 37*(12), e2023GB007789. https://doi.org/10.1029/2023GB007789

Schneider, K., & Erez, J. (2006). The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral Acropora eurystoma. Limnology and Oceanography, 51(3), 1284–1293. https://doi.org/10.4319/lo.2006.51.3.1284

Venn, A. A., Tambutté, E., Holcomb, M., Laurent, J., Allemand, D., & Tambutté, S. (2013). Impact of seawater acidification on pH at the tissue–skeleton interface and calcification—Journal of Science.

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., & Graham, N. A. J. (2019). Coral reef ecosystem services in the Anthropocene. Functional Ecology, 33(3), 531–539. https://doi.org/10.1111/1365-2435.13331